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Systematics and Zoogeography
of Middle American Shrews
of the Genus *Cryptotis*

BY

JERRY R. CHOATE

UNIVERSITY OF KANSAS
LAWRENCE
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INTRODUCTION

Short-tailed shrews of the genus *Cryptotis* occur in extreme southeastern Canada, throughout the eastern half of the United States, in all of México except the northwestern part, in Central America, and on the Andes of South America as far east as Venezuela and as far south as southern Ecuador. The genus was represented by a diverse and well-differentiated assemblage of species as early as the Pliocene, and differentiation apparently still is occurring. The altitudinal range of Recent species is from near sea level in the United States and northeastern México to above the level of forest vegetation in Central and South America. The species best known to neomammalogists in the United States, *Cryptotis parva*, is a common resident of mesic prairie habitat and of marshes and meadows within the eastern deciduous forest. Farther to the south, other representatives of the genus occur in arid scrub thickets, rainforests, grassy llanos, cloud forests, pine-oak forests, and páramo.

The present study was concerned only with the representatives of the genus *Cryptotis* that occur in Middle America as here defined—Central America and México, in addition to a few localities along the Río Grande in southernmost Texas. Arbitrary limitation of the research topic along political boundaries excluded part of the geographic range of one species, *C. parva*, the nominate subspecies of which does not occur in Middle America. South American taxa of *Cryptotis*, as well as United States populations of *C. parva*, will be reviewed in other reports.

Knowledge of the habits and relationships of members of the genus *Cryptotis* has lagged behind that of less secretive, more spectacular mammals. As a result, although the genus is represented by more than forty named kinds, it remains one of the least understood of the widely distributed American genera of mammals. Merriam (1895:6-8) summarized the early taxonomic history of the group; only 16 taxa were recognized at the time of his revision, nine of which he named as new. Subsequently, the number of available names from Middle America alone has increased to 34, but in the accounts beyond only 18 named kinds, representing eight species, are recognized.

The aims of this study were: to establish a usable classification of Middle American taxa of the genus *Cryptotis*; to delineate intra- and inter-specific patterns of variation; to summarize what is known of their distribution, ecology, and reproduction, and thus stimulate ecologically oriented research; to assess relationships of extinct to extant taxa; to interpret zoogeographic patterns; and through these

studies to stimulate additional collecting and application of bio-systematic and biometrical techniques for future consideration of the intricate interrelationships of these shrews.

MATERIALS AND ACKNOWLEDGMENTS

At the time of Merriam's (1895) review of *Cryptotis* (then considered a subgenus of *Blarina*), 219 specimens were available from Middle America and southernmost Texas. The majority of those specimens were part of the outstanding collection of birds and mammals amassed by E. W. Nelson and E. A. Goldman as a result of their exploratory studies in México for the Bureau of the Biological Survey. Three-quarters of a century later, only 735 conventionally prepared museum specimens have been available for study. The insubstantial increase in number of specimens underscores the importance of the collections made by Nelson and Goldman and is one of the principal reasons why shrews of the genus *Cryptotis* are so poorly known taxonomically and ecologically.

In addition to the 735 standard museum specimens (skins, skulls, and specimens in alcohol) examined, I have studied 1381 mandibles and partial crania from owl pellets or from Mayan ruins (denoted in lists of specimens examined by an asterisk). Also examined were approximately 50 fossils, representing all known extinct taxa of the genus *Cryptotis* as well as a closely related genus, *Paracryptotis*.

I am indebted to the curators of the following institutions, who placed specimens at my disposal. Abbreviations preceding names of institutions are used in the accounts beyond to identify the source of specimens.

ALG	Alfred L. Gardner (private collection)
AMNH	American Museum of Natural History, Richard G. Van Gelder and Sydney Anderson
ANSP	Academy of Natural Sciences of Philadelphia, R. R. Grant, Jr.
BMNH	British Museum (Natural History), J. E. Hill
CAS	California Academy of Sciences, Robert T. Orr
ENCB	Escuela Nacional de Ciencias Biológicas, Ticul Alvarez S.
FMNH	Field Museum of Natural History, Joseph C. Moore and Philip Hershkovitz
INAH	Departamento de Prehistoria, Instituto Nacional de Anthropología e Historia, Ticul Alvarez S.
JDS	James Dale Smith (personal collection)
KU	Museum of Natural History, The University of Kansas, J. Knox Jones, Jr.
LACM	Los Angeles County Museum, Donald Patten and Andrew Starrett
LSU	Museum of Zoology, Louisiana State University, George H. Lowery, Jr.
MCZ	Museum of Comparative Zoology, Harvard University, Barbara Lawrence
MVZ	Museum of Vertebrate Zoology, The University of California, W. Z. Lidicker, Jr., and Seth B. Benson
ROM	Royal Ontario Museum, Randolph L. Peterson and J. R. Tamsitt
TCWC	Texas Cooperative Wildlife Collection, Texas Agricultural and Mechanical University, William B. Davis and Dillford C. Carter

TNHC	Texas Natural History Collection, The University of Texas, Charles L. Douglas
UMMP	Museum of Paleontology, The University of Michigan, Claude W. Hibbard
UMMZ	Museum of Zoology, The University of Michigan, William H. Burt and Emmet T. Hooper
UNAM	Instituto de Biología, Universidad Nacional Autónoma de México, Bernardo Villa-R
USNM	United States National Museum, including the Biological Surveys Collection, Charles O. Handley, Jr., Henry W. Setzer, and R. H. Manville
WGB	W. Glen Bradley (private collection)

I am appreciative of grants-in-aid for museum visitations, as well as an 11-month traineeship and 3-month extension of that traineeship, from the National Science Foundation (Grant GB-4446X), administered by the Committee on Systematics and Evolutionary Biology at The University of Kansas. Support for field studies in Middle America was made available through a contract (DA-49-193-MD-2215) to Dr. J. Knox Jones, Jr., from the U.S. Army's Medical Research and Development Command. A grant from the Watkins Fund, The University of Kansas Museum of Natural History, enabled examination of specimens in México. Computer time allotted to me by the Department of Zoology enabled use of the GE 635 computer at The University of Kansas Computation Center.

I am especially grateful to Dr. J. Knox Jones, Jr., who supervised the research, examined holotypes and other specimens for me at the British Museum (Natural History), and critically reviewed the manuscript. Drs. Robert S. Hoffmann and Charles O. Handley, Jr., also reviewed the manuscript, and the latter made numerous helpful suggestions during the course of the research.

Several other persons deserve acknowledgment because of assistance or advice rendered. Foremost of those is Dr. Claude W. Hibbard, who spent considerable time in direct communication and correspondence regarding relationships of fossil shrews. Of the graduate students at Kansas, Hugh H. Genoways, Carleton J. Phillips, and James Dale Smith have been especially helpful; Smith assisted with statistical programs and analyses. Others with whom beneficial discussions were held include Dr. Guy G. Musser, Dr. Sydney Anderson, Sr. Ticul Alvarez S., and Dr. E. Raymond Hall, under whose guidance the study was begun.

Finally, I especially acknowledge my wife, Fi, who prepared the illustrations, contributed valuable clerical assistance, and provided the encouragement needed to complete the study.

METHODS

The preliminary step in a study such as the one undertaken here necessarily is to derive an estimate of intra-populational variation in a known species for which an adequate sample is available. I chose for this purpose a large sample of *C. mexicana* from the highlands of Veracruz. Specimens from that sample were grouped separately according to sex and age, but subsequent statistical tests demon-

strated the feasibility of pooling mensural data from males and females of all ages (excepting nest young and atrophic old adults).

Using intra-populational variability in *C. mexicana* as a guideline, a search for useful taxonomic characters was undertaken. All the holotypes of Middle American taxa of *Cryptotis*, as well as the published diagnoses of each, were studied and distinctive features of each holotype were compared. Characteristics by which the holotypes differed then were tested by comparison with series of paratypes. It was discovered that many characters used by previous authors (as well as some devised by me) to discriminate between species are attributable to seasonal or other sources of infraspecific variation. Subsequent examination of holotypes and paratypes, however, revealed cranial, dental, and pelage characteristics by which eight nominal species can be distinguished. Illustrations of some of these characters were prepared by means of a Wild Heerbrugg Stereomicroscope to which a drawing tube had been fitted.

Having estimated intra-populational variability and established a series of interspecific characters, external, cranial, and dental measurements were selected for subsequent analyses of non-geographic and geographic variation. In the following accounts, measurements of total length, length of tail, and length of hind foot are those recorded by the collectors. Cranial measurements were taken by me with an ocular micrometer in a binocular microscope ($15 \times$ magnification) to which a movable platform and vernier scale were attached. All external and cranial measurements are in millimeters, and weights are in grams. Cranial measurements are defined below and illustrated in Fig. 1.

Condyllobasal length (a).—From the anterior surface of the fused premaxillae at a point midway between the falciform incisors to the posterior surface of the occipital at a point midway between the occipital condyles. This measurement can be taken accurately only if all extraneous tissue has been removed from between the incisors. The anterior surface of the fused premaxillae is convex in some specimens and concave in others; the measurement always was taken from the midpoint.

Palatal length (b).—From the anterior surface of the fused premaxillae (as in condyllobasal length) to the posterior surface of the hard palate at a point midway between the pterygoid processes. In some specimens the posterior surface of the hard palate is convex, in some it is concave, and in occasional specimens a posteriorly projecting process is situated midway between the pterygoids. When a

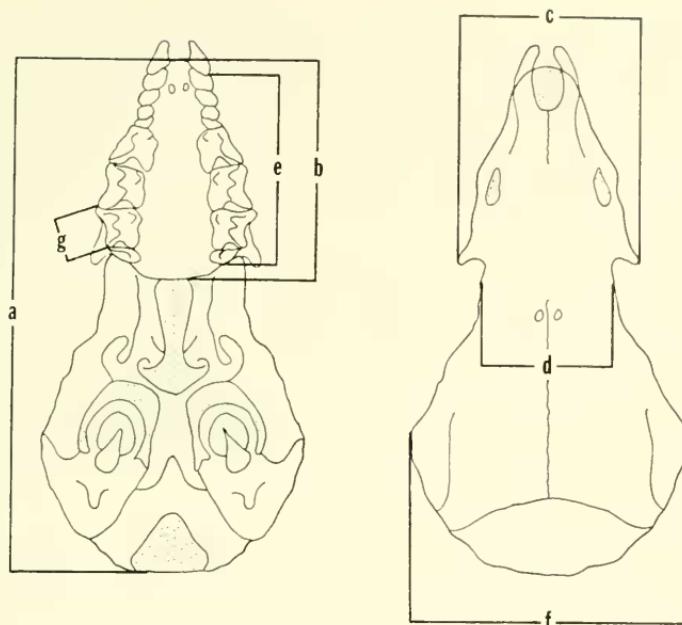


FIG. 1. Skull of *Cryptotis goldmani alticola* (KU 112039) showing measurements described in text. Interorbital breadth (d) is illustrated on the dorsal view of the skull, but in practice was measured from the ventral aspect (see text).

process was present, the measurement was taken to one side or the other; otherwise, it was taken from the midpoint.

Maxillary breadth (c).—Distance between the lateral tips of the zygomatic processes of the maxillaries. Specimens in which one or both processes were broken were not measured. Also, old adults having obviously atrophic processes were not measured.

Interorbital breadth (d).—The breadth of the interorbital region at a point level with the posterior surface of the hard palate.

Maxillary toothrow (e).—From the labial point of juncture of the crowns of the falciform incisor and first upper unicuspis to the posterior surface of the third upper molar. In a few specimens having no contact between the incisor and unicuspis the measurement was taken from the posterior surface of the falciform incisor.

Cranial breadth (f).—Greatest lateral breadth of the braincase.

Length of M2 (g).—From the anterior surface of the parastyle to the posterior surface of the metastyle, taken parallel to a plane passing through those two points. A slightly different reading would result if the measurement were taken parallel to the plane of the maxillary toothrow or to the long axis of the skull.

Various authors (for example, Jackson, 1928:14), have commented

on the necessity for consistency of technique when studying color of mammals having iridescent hair. It is important not only that the light be of approximately the same intensity and that it strike the specimens at the same angle, but also that each specimen be viewed from the same angle. For example, representatives of the *mexicana*-group of the genus *Cryptotis* appear distinctly more grayish (less reddish) when viewed from the posterior end as opposed to the anterior end because of added visual effect of the basal gray region of the pelage. Jackson (1915:20) tried to overcome this problem in his study of moles by consistently viewing specimens from the anterior end, but he (1928:14) reversed the angle of view in his study of shrews in the genus *Sorex*. In *Cryptotis*, I consider the coloration of the tips of the hairs to be more useful taxonomically than the combined effect of coloration of tips and basal region, so I viewed specimens from the anterior end.

Optimally, examination of color of mammals with iridescent pelage should be performed with a constant source of light, but examination of specimens at different museums (using various sources of light and receiving reflection from various background surfaces) precludes absolute uniformity. My standard procedure was to place specimens on a white surface and examine them from above the anterior end at an angle of about 45°, with a white fluorescent lamp located directly overhead as the primary source of light.

Capitalized color terms used herein are from Ridgway (1912). Liberal use was made of comparative terminology when it was impossible to match colors of specimens with those of Ridgway. No attempt was made to characterize color accurately in certain taxa because available specimens are not suited for that purpose as a result of unsatisfactory preparation or changes in color subsequent to preparation.

My observations on foxing in *Cryptotis* agree fully with Meester's (1963:2) comments on foxing in shrews of the genus *Crocidura* in southern Africa. Specimens that have been in collections for several decades, such as the excellent series from México that was collected around the turn of the century by Nelson and Goldman, are reddish brown in color; these same specimens, however, were described by Merriam (1895) as "dusky or sooty black" or "sooty brown." Obviously, as a result of foxing, there has been a substantial change in color from black or dark brown to reddish brown. Another example concerns the holotype of *C. mexicana madrea*, which Goodwin (1954a:1) characterized as "blackish . . . less reddish than specimens . . . from Jico, Veracruz," but which, only 15 years later, is more

distinctly reddish than any other specimen of *mexicana* examined. Because of the uncertainties regarding rapidity and degree of foxing, it was not considered prudent, unless recently collected specimens were available for comparison, to utilize precise standards of color nomenclature to describe differences that may simply be a function of time in preservation or the kind of fumigants used to protect collections.

Methods of statistical analysis used in this study were selected for their utility and ease of interpretation, and have been described in greater detail by Smith (1969). The logic underlying most of the testing procedures used is discussed by Sokal and Rohlf (1969). Initial analysis involved computation of standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation) for all specimens of a species from each of several individual or pooled localities. Males and females were considered separately to assess differences resulting from secondary sexual variation, and the different age categories were treated in like manner to determine the effects of variation with age. When two or more group-means were compared, a single classification analysis of variance was used to test (*F*-test, .95 level of confidence) for significant differences among means. A program (UNIVAR) that was discussed by Power (1970), and which makes use of Gabriel's (1964) Sum of Squares Simultaneous Test Procedure (SS-STP), was employed to determine maximum non-significant subsets (groups of means), and thereby facilitate interpretation of trends in variation of individual characters. Multivariate analyses were conducted by means of a revised version of the Classical Numerical Taxonomy System (CLNTS-Version 2) at The University of Kansas. This program was used to generate taxonomic distance coefficients among samples from standardized character values, as well as phenograms based on UPGMA (unweighted pair-group method using arithmetic averages). The distance matrices and phenograms facilitated interpretation of overall similarities between Operational Taxonomic Units (OTUs), which in the case of geographic variation corresponded to standardized sample means.

Because of the paucity of series adequate for statistical analyses, it often was necessary to pool data from nearby localities. Samples of the four geographically variable species of *Cryptotis* in Middle America were pooled as shown below; localities are listed in abbreviated form, but precise localities can be found in lists of specimens examined.

Cryptotis mexicana

Sample 1.—TAMAULIPAS: Gómez Fariás. VERACRUZ: Zacualpan. QUERÉTARO: Pinal de Amoles. HIDALGO: Encarnacion; Molango; Zalcuitalpan; Acaxochitlán; Tulancingo. PUEBLA: Honey.

Sample 2.—HIDALGO: Tenango de Doria. PUEBLA: Villa Juárez; Huauchinango; Xocoyolo; Zacapoaxtla.

Sample 3.—VERACRUZ: Tlapacoyan; Jalacingo; Las Vigas; La Joya; Jalapa; Xico; Teocelo.

Sample 4.—VERACRUZ: Huatusco; Coscomatepec; Orizaba.

Sample 5.—VERACRUZ: Volcán San Martín.

Sample 6.—OAXACA: Papalo Santos Reyes; Vista Hermosa; Llano de las Flores; Ixtlan de Juárez; Cerro San Felipe.

Sample 7.—OAXACA: Totontepec; San Pedro Cajonos; Cerro Zempoaltepec; “Colonia Rudolfo Figueroa.”

Sample 8.—OAXACA: Oaxaca de Juárez; Sola de Vega; Santos Reyes Nopala; San Miguel Suchixtepec; Lovene.

Cryptotis goldmani

Sample 1.—MICHOACÁN: Cd. Hidalgo. ESTADO DE MÉXICO: Salazar; Cerro Ajusco; Lagunas de Zempoala; Amecameca; Nevado de Toluca; Volcán Popocatépetl. DISTRITO FEDERAL: Bosenchere; Cerro de Santa Rosa; Cañon Contreras.

Sample 2.—JALISCO: Autlán; Cd. Guzmán; Volcán de Fuego; Nevado de Colima. MICHOACÁN: Cerro Tancítaro.

Sample 3.—GUERRERO: Omilteme; Chilpancingo.

Sample 4.—OAXACA: Vista Hermosa; Llano de las Flores; San Andres Chicahuaxtla; Cerro Zempoaltepec; Mixtequila; Tehuantepec; Lachao; Santa María Ozolotepec; San Juan Ozolotepec; San Miguel Suchixtepec.

Sample 5.—CHIAPAS: San Cristóbal de las Casas.

Sample 6.—GUATEMALA: Todos Santos Cuchumatán.

Cryptotis parva

Sample 1.—TEXAS: Del Rio; Brownsville. COAHUILA: Melchor Múzquiz. TAMAULIPAS: Camargo; Matamoras.

Sample 2.—TAMAULIPAS: Cd. Victoria; Piedra; Ocampo; Gómez Fariás; Altamira. SAN LUIS POTOSÍ: El Salto; Platanito; Alvarez.

Sample 3.—NAYARIT: Tepic. JALISCO: Guadalajara; Mascota; Huáscata; Ocotlán. GUANAJUATO: Guanajuato. MICHOACÁN: Cumuato; La Palma; Quiroga; Pátzcuaro; Morelia; Rancho Baralosa.

Sample 4.—ESTADO DE MÉXICO: San Juan Zitaltepec; Tlapacoyán. DISTRITO FEDERAL: Bosque Chapultepec; Tlalpan.

Sample 5.—SAN LUIS POTOSÍ: Xilitla; Huichihuayán. VERACRUZ: El Brinco. PUEBLA: Metlaltoyuca; Villa Juárez; Huauchinango.

Sample 6.—VERACRUZ: Jalapa; Xico; Cerro Gordo; Teocelo; Boca del Río; Mecayucan; Cordoba; Orizaba; Catemaco.

Sample 7.—OAXACA: Teotitlán del Camino; Tuxtepec; Choapan; Putla; Santiago Lachiquiri; Sola de Vega; Sta. Catarina Juguila; San Gabriel Mixtepec; Puerto Escondido; San Miguel Suchixtepec; San Agustín Loxicha; Pluma Hidalgo.

Sample 8.—CHIAPAS: Yajalón; Pueblo Nuevo Solistahuacán; San Cris-

tóbal de las Casas; Volcán Kagchiná; Cueva Los Llanos; Comitán; Villa Flores; Prusia; Finca Esperanza; Huixtla.

Sample 9.—GUATEMALA: La Primavera; Panajachel.

Sample 10.—HONDURAS: Lago de Yojoá; Belén; Cerro Cantoral; Yuscarán. EL SALVADOR: Cerro Montecristo. NICARAGUA: San Raphael del Norte.

Sample 11.—COSTA RICA: Cinchona; Zarcerio; “Irazú Range”; Finca Coliblanca; San José; San Pedro Montes de Oca; Estrella; Cartago; Cerro Tablazo; El Muñeco; “Guarco.” PANAMÁ: Santa Clara; Cerro Punta-Boquete trail.

Cryptotis nigrescens

Sample 1.—YUCATÁN: Mérida; Chichén Itzá; Uxmal; Xbac. QUINTANA ROO: Laguna de Chichancanab. CAMPECHE: La Tuxpeña. BRITISH HONDURAS: Baking Pot. GUATEMALA: Uaxactún.

Sample 2.—CHIAPAS: Volcán Kagchiná; Cueva Los Llanos. GUATEMALA: Jacaltenango; La Primavera. HONDURAS: San José; Las Flores; Yuscarán. EL SALVADOR: Cerro Cacaquatique.

Sample 3.—COSTA RICA: Tilarán; San Isidro de El General; Volcán Irazú. PANAMÁ: Cerro Punta; Volcán de Chiriquí; Santa Clara.

Sample 4.—PANAMÁ: Cerro Tacarcuna; Cerro Malí; Cerro Pirre.

The arrangement of species in the accounts that follow is more or less from the most generalized forms to those most specialized within species-groups. The first two species-groups (the *mexicana*-group and *parva*-group) probably are monophyletic, whereas the third group (Relict species) consists of three primitive species with uncertain phylogenetic affinities. The species-groups have no formal taxonomic significance and are discussed following the accounts of species. Subspecies are arranged alphabetically within species.

The first citation in synonymies is to the original description, which I have consulted in every instance. The second citation is to the first usage of the name combination presently employed if it differs from the name as originally proposed. Next is a chronological listing of other names and name combinations that have been applied in the literature to the taxon as here recognized. I have cited only those publications in which specimens and precise localities are listed (excluding simple reference to type localities); the single exception is Hall and Kelson's (1959) "The mammals of North America." The latter is included because it is the most recent compilation of literature on distribution of North American representatives of the genus *Cryptotis* and, therefore, is the reference most likely to be consulted for information relating to prior research. Subjective synonyms in synonymies include designation of type locality. The word "part" appears italicized and in parentheses after an entry in synonymy if the name was applied only in part to the taxon as here

recognized. Entries were made occasionally in synonymies solely because they were pertinent to the historical background of the taxon.

Middle American countries, states of México, and localities within Mexican states and Central American countries are arranged from north to south in lists of specimens examined. When two or more localities are at the same latitude, they are arranged from west to east. Departamentos of Central American countries are not indicated in lists of specimens examined, but are in the gazetteer. Localities in italics were not plotted on distribution maps because undue crowding would have resulted.

COMMENTS ON TAXONOMIC CHARACTERS

Dental formula.—Embryological studies, reviewed by Choate (1968:252) and Meester (1963:10), to determine homologies of the so-called "unicuspids" of shrews are not in agreement. Repenning's (1967:3) suggestion to refer to all teeth situated between the first incisors and molars as "antemolars" is almost as indefensible as Merriam's (1895:5) arbitrary designation of homologies; the former conceals the fact that the "fifth upper and second lower antemolars" in *Cryptotis* are known beyond any reasonable doubt to represent P4 and p4, respectively. In the sincere hope that future studies will show convincingly the homologies of teeth in shrews, I have attempted to avoid the problem of semantics by retaining use of the term "unicuspid" and by referring to the normal dental formula for Recent shrews of the genus *Cryptotis* as:

$$\begin{array}{l} 1 \text{ (falciform incisor)} \quad - 4 \text{ (unicuspids)} - 1 \text{ (P4)} - 3 \text{ molars} \\ \hline 1 \text{ (procumbent incisor)} - 1 \text{ (unicuspid)} - 1 \text{ (p4)} - 3 \text{ (molars)} \end{array}$$

This formula was derived by loss of one upper unicuspid (probably P3) from the primitive soricid dental formula (1-5-1-3/1-1-1-3), which was intact in at least one Pliocene representative of the genus *Cryptotis* and is retained in a related genus, *Blarina*. A strong tendency toward further reduction of the formula to 1-3-1-3/1-1-1-3 is exhibited by certain populations of *C. mexicana*.

Bulbous dentition.—Bulbous teeth have convex rather than straight sides and are robust in appearance. They give the impression of being particularly well adapted for crushing, as opposed to shearing or cutting by non-bulbous teeth, and are resistant to wear. The first three upper unicuspids in taxa having bulbous teeth typically are enlarged and disproportionately robust, whereas the fourth typically is reduced in size and peglike in appearance. The postero-

lingual basal cusplets of the upper unicuspids likewise are reduced or sometimes lacking. Bulbous upper molars tend to be almost square in occlusal outline, and the posterior surfaces of P4-M2 are only slightly, if at all, emarginate. Probably the primitive condition is somewhere between the extremes of bulbous and non-bulbous dentitions; the extremes undoubtedly have evolved independently in several lineages and considerable geographic variation in tooth structure occurs in certain wide-ranging species.

Posterior surfaces of P4-M2.—The first and second upper molars primitively were almost square in occlusal outline, and their posterior surfaces, as well as that of the fourth upper premolar, were not emarginate. Adaptations to permit efficient shearing or cutting have resulted in reduction or loss of the hypocone, lingual expansion and specialization of the hypoconal basin, and a tendency for emargination of the posterior surfaces on the upper molariform teeth. The degree of emargination arbitrarily has been described herein by the comparative terms "considerably," "moderately," "slightly," or "not at all." Although certain species exhibit marked geographic variation of this characteristic, it remains a useful means of describing one aspect of specialization of non-bulbous teeth.

Protoconal and hypoconal basins.—The protoconal basin is defined herein as the basin-shaped region of each upper molariform tooth that separates the protocone from the paracone and metacone. The hypoconal basin is the basin-shaped region between the hypocone (which is vestigial and consists merely of an elevation on the lingual lip of the basin) and metacone. Comparisons of protoconal and hypoconal basins in accounts provide an index to one or the other of two evolutionary events: reduction (antero-posterior compression) of the protoconal basin, and postero-lingual expansion of the hypoconal basin. Primitively the two basins were approximately the same size; reduction of the protoconal basin was related to reduction in length of toothrow, whereas expansion of the hypoconal basin was not associated directly with length of toothrow because expansion was in the postero-lingual direction and did not necessarily involve elongation of the tooth.

Cristae of upper molars.—To my knowledge, no names previously have been applied by students of Recent mammals to the crests that connect the styles and cones on the ectoloph of each upper molar in taxa that retain the basic tribosphenic pattern. Appropriate, although somewhat cumbersome, terms were proposed for extinct mammals by Van Valen (1966:7-9), as follows: the *paracrista* is the crest that connects the parastyle and paracone; the *precentrocrista*

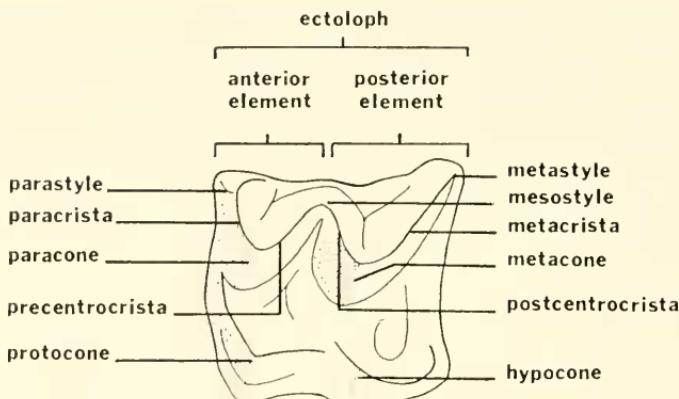


FIG. 2. First left upper molar of *Cryptotis magna* (KU 99542) illustrating dental terminology used in text.

connects the paracone and mesostyle; the *postcentrocrista* connects the mesostyle and metacone; the *metacrista* connects the metacone and metastyle (Fig. 2). Primitively, the arrangement of crests resulted in the typical dilambdodont structure of each of the upper molars, but reduction or elimination of certain of the posterior crests and cusps has obliterated the primitive pattern on M3 of all but the most unspecialized dentally of Recent taxa of *Cryptotis*, as discussed below.

Homologies of cusps on M3.—Interpretations of homologies of cusps on the third upper molars of soricids differ from author to author. The following comparison of suggested homologies is from H. H. T. Jackson's review of the American long-tailed shrews (genus *Sorex*) and Jurgens Meester's revision of the genus *Crocidura* in southern Africa:

	Jackson (1928:15)	Meester (1963:29)
Labial cusp	paracone	parastyle
Central cusp	mesostyle	paracone
Two posterior cusps	metacone	mesostyle
Postero-lingual cusp	not named	metacone
Antero-lingual cusp	protocone	protocone

One reason for past confusion regarding homologies of cusps on M3 is that in both *Sorex* and *Crocidura* that tooth is relatively reduced and specialized. In *Cryptotis*, however, the species recognized here form a linear sequence of specialization ranging from the primitive complement and arrangement of cusps to a situation in which these are highly reduced, thus homologies are evident (Fig. 3).

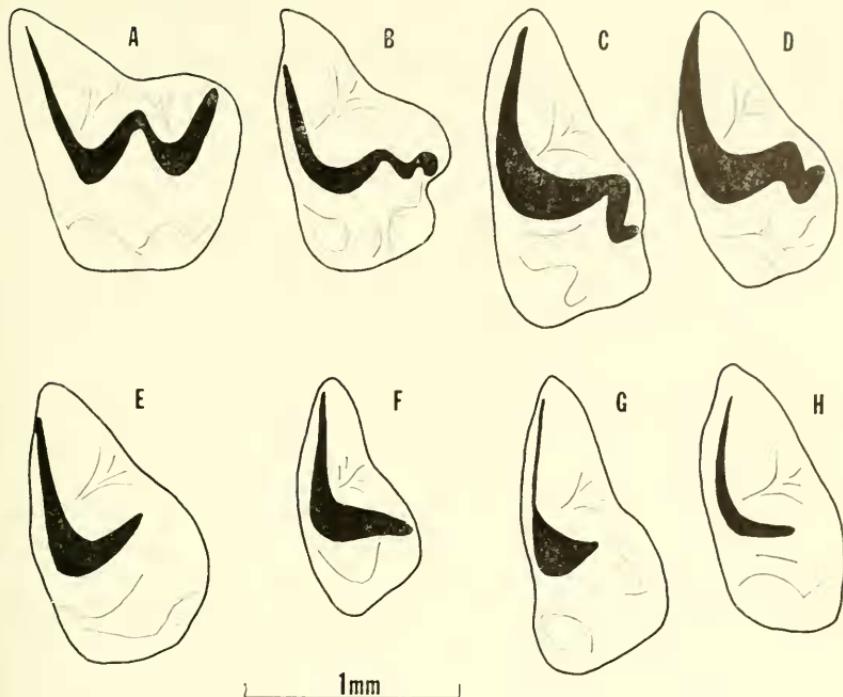


FIG. 3. Sequence (semi-diagrammatic) of reduction and specialization of the ectoloph of the third upper molar in *Cryptotis*: A, hypothetical blarinine ancestor; B, *C. gracilis* (KU 106941); C, *C. magna* (KU 99542); D, *C. mexicana mexicana* (KU 23413); E, *C. nigrescens merriami* (KU 84365); F, *C. parva pueblensis* (KU 23415); G, *C. goldmani alticola* (KU 112039); H, *C. goodwini* (KU 64610). The upper third molar of *C. endersi* (not illustrated) is similar to that of *C. gracilis*. Note also changes in overall configuration of tooth.

—compare with Fig. 2). My interpretation of homologies agrees with that of Meester (*loc. cit.*).

Zygomatic plate.—In *Cryptotis*, as in other mammals, the zygomatic plate is derived at least in part from the maxillary bone, and forms the outer wall of the infraorbital canal. Its placement in *Cryptotis* varies functionally and phylogenetically with the placement of the maxillary process, which also is a vestige of the zygomatic arch. The anterior and posterior borders of the zygomatic plate are well-defined; their placement with respect to the toothrow can be described with reference to M3 or to one or another of the three prominent styles on the labial surface of either M1 or M2. Primitively, the maxillary process was situated farther anteriorly with respect to the toothrow (possibly as far as directly above M2) than in most Recent taxa. Accordingly, the anterior border of the zygomatic plate was above, or slightly anterior to, the parastyle of

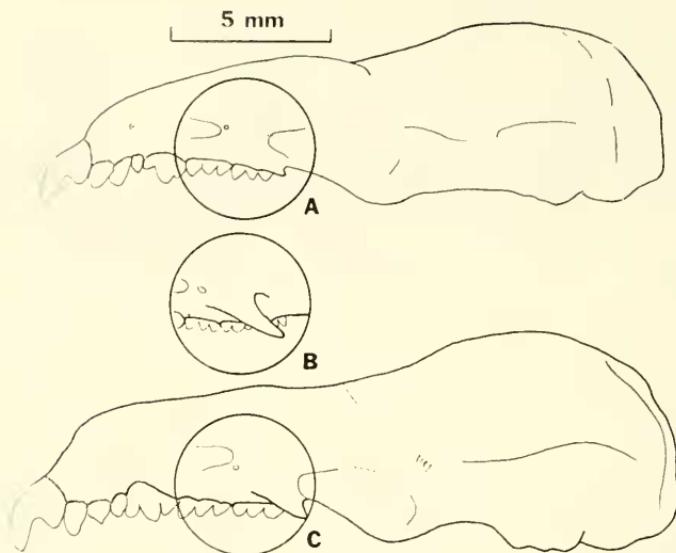


FIG. 4. Comparison of position and structure of the zygomatic plate in (A) *C. parva pueblensis* (KU 23415) and (C) *C. mexicana mexicana* (KU 23413). The inset (B) represents a hypothetical blariniine ancestor.

M1, and the posterior border was above, or anterior to, the mesostyle of M2. In the most advanced Recent taxa, as well as highly specialized extinct species, the anterior border is situated above the junction of M1 and M2, whereas the posterior border is posterior to the zygomatic process and approximately above M3 (Fig. 4).

Arrangement of cusps on ectoloph of M1.—Although the arrangement of stylar cusps is similar on M1 and M2, M1 was selected for reference because slight antero-posterior compression of M2 tends to conceal otherwise distinctive characteristics. The anterior and posterior stylar cusps (the parastyle and metastyle, respectively) of M1 and M2 undergo independent embryonic development, as shown for bats by Marshall and Butler (1966) and Phillips (1969), and possibly are subject to independent genetic control. Each of the anterior and posterior elements of the ectoloph contributes to the mesostyle, and fusion is not complete in occasional specimens of *Cryptotis* and most specimens of *Blarina*. In labial view, the valley separating the parastyle and mesostyle of M1 may be narrower than or as broad as the valley separating the mesostyle and metastyle. This characteristic is referred to in diagnoses by comparing the extent of reduction of the anterior element of the ectoloph of M1 relative to the posterior element.

Talonid of m3.—Repenning (1967:39) mistakenly assumed that a

reduced talonid, consisting of only one cusp, on the third lower molar is a generic characteristic of *Cryptotis*. Actually, the talonid of m3 in *Cryptotis* exhibits considerable variation as to degree of reduction and specialization; it varies from the primitive condition, in which the talonid is elongate and bears a pronounced hypoconid and entoconid, to the opposite extreme, in which the talonid is short and narrow and consists only of a vestigial hypoconid.

Vermiculations.—The hair of certain representatives of the genus *Cryptotis* (and of other shrew genera) has a structural peculiarity that is visible to the naked eye. When one blows on the pelage to separate the hairs, a series of pale rings or bands, which were termed "vermiculations" by Jackson (1915:11), can be seen in the gray basal region. With magnification, vermiculations can be seen to correspond to kinks in the pelage, and probably are related to differential refraction of light by curved, as opposed to straight, regions of individual hairs. Vermiculations are more numerous in long winter pelage than in short summer pelage, and are more distinctive in populations inhabiting cool forests at high elevations than in populations from lower elevations. The functional significance of vermiculations in moles has been related to their fossorial habits; Jackson (*loc. cit.*) suggested that vermiculations are related to the capacity of mole pelage to lay almost equally well either forward or backward. Accordingly, certain species of *Cryptotis*, such as *C. goldmani*, that demonstrate pronounced vermiculations and have lax, molelike pelage have been suggested by collectors to be semi-fossorial in habits. Furthermore, those species in which vermiculations are most prominent also are characterized by well-developed forefeet and claws.

NON-GEOGRAPHIC VARIATION

Variation with Age

In temperate regions of North America, shrews are born in spring or summer, usually reach sexual maturity the following spring, and rarely survive through a second winter. As a consequence, specimens collected in spring or summer represent three relatively distinct age classes: subadults (recently born); adults (first year animals); and old adults (second year animals) (see, among others, Pearson, 1945, on *Blarina brevicauda*; Hamilton, 1940, on *Sorex fumeus*; Conaway, 1952, on *Sorex palustris*; Findley, 1955b, on *Sorex vagrans*). Working with *Blarina*, Choate (1968:253) was able to distinguish four age categories, apparently corresponding to spring and summer litters of each of the two potential years of life.

Times of reproductive activity in Middle American representatives of the genus *Cryptotis* are not well known, and it is likely that some populations reproduce throughout the year. Specimens in collections superficially show almost continuous gradations of dental attrition, but when condition of pelage (see section beyond) is taken into account the following age categories, albeit arbitrary, can be defined:

Young.—Teeth unworn; juvenal pelage.

Subadult.—Crests and cusps of teeth slightly worn only on tips; fresh adult pelage or molting from juvenal to adult pelage.

Adult.—Teeth noticeably worn; adult pelage.

Old adult.—Cutting surfaces worn to base level; adult pelage.

Because the deciduous dentition of *Cryptotis* is shed prior to birth, "juveniles," defined by that criterion, occur only *in utero*. "Young" are recently weaned and still in juvenal pelage. In most species, wear on teeth becomes apparent at about the time of the post-juvenile molt, thus clearly delimiting the "subadult" category, but wear is not readily apparent until much later in representatives of species characterized by bulbous dentition. Criteria employed to distinguish between "subadults" and "adults" were adequate for most specimens, but assignment of a few borderline individuals to one or the other category was arbitrary on the basis of information gleaned from examination of other specimens in the series. Likewise, a few specimens were not readily assignable to one or the other of the "adult" or "old adult" categories, thus necessitating arbitrary designation.

The largest sample available (excluding samples from owl pellets and archaeological sites) of any of the taxa of Middle American *Cryptotis* was selected for study to determine which age categories, if any, could be pooled for analysis of geographic variation in external and cranial dimensions. Nest young and obviously atrophic old adults were excluded from the sample and from all subsequent analyses. Thus restricted, the sample consisted of 85 specimens (16 young, 20 subadults, 32 adults, and 17 old adults) of *C. mexicana* from eight localities in the vicinity of Jalapa, Veracruz.

A significant difference ($P < .01$) among age categories was found for only one measurement, length of maxillary toothrow. Coefficients of variation for measurements of length of toothrow in many instances were higher than for other cranial measurements, possibly indicating that measurement is subject to sources of variability not considered in this analysis. The maxillary toothrow apparently is longest early in life, and decreases in length with increased age.

Other external and cranial measurements did not differ significantly ($P > .05$) with age; thus, specimens of all ages (excluding nest young and visibly atrophic old adults) were considered together in analyses of geographic variation.

I realize that lack of significant morphometric variation with age in a single population of *C. mexicana* may not indicate lack of variation with age in other species, or even in other populations of the same species from another part of its geographic range. However, no other samples of Middle American *Cryptotis* presently are large enough to permit comparable analyses.

Secondary Sexual Variation

Various authors, the most recent being Dapson (1968:125-126) in his study on *Blarina*, have alluded to slight secondary sexual variation in size in some species of American shrews, whereas others, notably Jackson (1928:20) and Findley (1955b:7) in their studies on *Sorex*, found none. To determine whether secondary sexual differences contribute to morphometric variation in *Cryptotis*, the same sample, with few exceptions, of *C. mexicana* that was used for analysis of variation with age was tested. The sample consisted of 82 specimens (39 males and 43 females) collected (and sexed) primarily by W. W. Dalquest, E. A. Goldman, and E. W. Nelson. A significant difference ($P < .05$) between males and females (females being the larger) was found for only one measurement, length of maxillary toothrow, the only measurement for which significant variation with age was demonstrated. Other measurements did not exhibit significant ($P > .05$) secondary sexual variation, and so far as I know there are no secondary sexual differences in proportions, color, or any other characters of taxonomic import in Middle American shrews of the genus *Cryptotis*. Males, females, and specimens for which no determination of sex was made by the collector thus were considered together in analyses of geographic variation.

Individual Variation

Individual variation, here defined to include all variability not attributable to age, sex, season, or place of capture, may be subdivided into "abnormal" and "normal" individual variation. The former, as distinguished from the latter, involves unusual variability resulting from random selection from the gene pool of a species, as well as developmental abnormalities. Some kinds of variability may be "normal" for one or more populations of a species but "abnormal" for the species as a whole, and arbitrarily are classified in the latter category.

"Abnormal" individual variation.—Abnormal variation in pigmentation of pelage apparently is infrequent in *Cryptotis*. Elder (1960:506-507) reported a completely albinistic individual of *C. parva* from Missouri, and I examined a specimen (USNM 347435) of *C. parva* from Texas that lacks pigment in the hairs except in the basal gray region, which appears normal. Although no albinistic specimens were seen from Middle America, 24 specimens of *C. mexicana*, two of *C. goldmani*, and one of *C. nigrescens* were found to have scattered clusters of hairs that lack pigment at the tips. With respect to *mexicana*, the highest incidence of white-tipped hairs was in specimens from localities on the southern part of the Sierra Madre Oriental and on the Sistema Montañoso.

Dental abnormalities also were infrequent except in specimens of *mexicana* from the coastal range of southern Oaxaca, almost all of which lack one or both of the fourth upper unicuspids. One or both of a pair of upper unicuspids also were missing from three specimens of *mexicana* from other populations, and from three specimens of *nigrescens*, two of *parva*, and one of *goodwini*. Other abnormalities found include: one specimen of *parva* (JDS, uncatalogued owl pellet material) with enormously robust parastyles on both second upper molars, causing those teeth to be markedly distorted; one specimen of *mexicana* (USNM 68553) with a bicuspidate third right upper "unicuspid"; and one specimen of *gracilis* (LSU 12655) that lacks all but a hint of dental pigmentation.

"Normal" individual variation.—The extremes and "means" for coefficients of variation for each of 10 measurements of all Middle American taxa of *Cryptotis* considered together are shown in Fig. 5. As illustrated, "means" are simple arithmetic means of coefficients of variation for all populations studied; they should not be interpreted as average coefficients of variation in a statistical sense, but are included to indicate trends in variability among the 10 characters. External measurements, which were taken by different field collectors, probably in slightly different ways, are more variable than cranial measurements, all of which were taken by me. Length of tail is the most variable measurement tested, possibly reflecting the fact that the pelvic girdle in shrews is situated at the extreme posterior end of the trunk (it is farther anterior in most other mammals) and interferes with measurement of the tail. Length of the second upper molar is the most variable cranial or dental measurement even though the extremes of samples tested seldom exceeded 0.2 mm. This apparent anomaly is due to the relatively large unit of measure (0.1 mm.) utilized; in order to reduce the coefficient of variation for

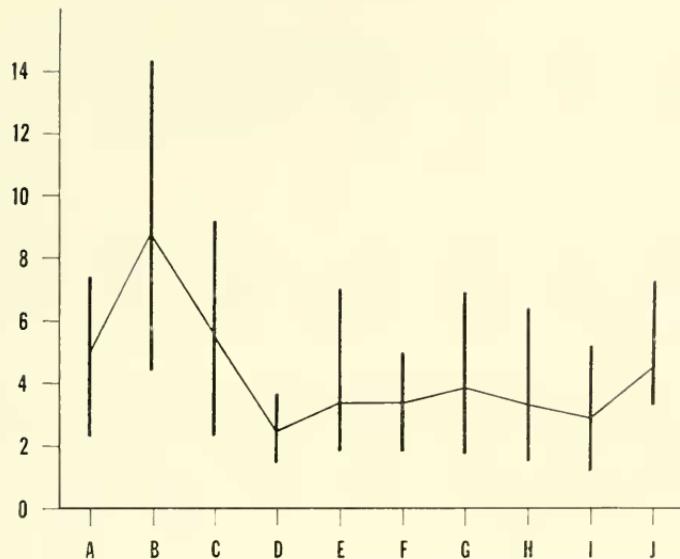


FIG. 5. Extremes and "means" (see text) of coefficients of variation (vertical axis) for each of 10 measurements (horizontal axis) of all Middle American taxa of *Cryptotis* considered together. A, total length; B, length of tail; C, length of hind foot; D, condylobasal length; E, palatal length; F, maxillary breadth; G, interorbital breadth; H, length of maxillary toothrow; I, cranial breadth; J, length of M2.

length of M2 to a level comparable to those of other cranial and dental measurements, it would be necessary to measure the length of M2 at least to the nearest 0.01 mm. Variation in other cranial and dental measurements is consistently low, particularly considering the small size of certain samples tested (Table 1).

Seasonal Variation

The most conspicuous source of seasonal variation is related to differences in color and texture of seasonal pelages. These differences, however, can be understood fully only when sufficient information is available as to the actual process of molt.

Most data on molt in *Cryptotis* are from *C. parva* in the United States, but other Middle American species apparently conform to the same patterns. Furthermore, with few exceptions the patterns exhibited by *Cryptotis* are similar to those of other North American soricids (see Conaway, 1952, on *Sorex palustris*; Findley, 1955b, on *S. vagrans*; Hamilton, 1940, on *S. fumeus*; Jackson, 1928, on *Sorex* in general; and Findley and Jones, 1956, on *Blarina brevicauda*).

The post-juvenile molt of *Cryptotis* (unlike that of *Blarina*, see Findley and Jones, *op. cit.*), is not uniform regardless of whether it

TABLE I.—Measurements of Middle American *Cryptotis*. Numbers in parentheses following identification of taxa refer to sample numbers for polytypic species as listed in Methods and Materials. The first line for each measurement includes the mean plus or minus two standard errors, the second line the extremes, and the third line the coefficient of variation and the number of specimens examined (in parentheses).

Total length	Length of hind foot	Condylar basal length	Palatal length	Maxillary breadth	Interorbital breadth	Maxillary toothrow	Cranial breadth
<i>C. mexicana mexicana</i> (2), vicinity of Huauchinango, Puebla, and adjacent Hidalgo							
99.0±1.94 93–109 4.6 (22)	13.9±0.30 12–15 5.0 (22)	19.2±0.37 18.3–19.9 2.7 (8)	8.3±0.20 7.8–8.5 3.5 (9)	6.2±0.10 5.8–6.6 3.4 (17)	5.0±0.07 4.7–5.4 3.0 (20)	6.9±0.11 6.5–7.4 3.4 (18)	10.2±0.10 9.7–10.6 2.2 (20)
99.7±0.85 89–108 3.7 (78)	13.3±0.21 11–17 7.1 (80)	19.0±0.12 18.1–19.9 2.3 (56)	8.1±0.08 7.2–8.8 3.9 (70)	6.1±0.05 5.8–6.6 3.4 (73)	4.9±0.03 4.7–5.3 2.9 (81)	6.8±0.10 5.8–7.5 6.2 (77)	10.1±0.06 9.7–10.6 2.3 (67)
96.1±1.16 92–100 2.3 (14)	13.0±0.16 12.5–14.0 2.4 (14)	18.9±0.31 18.5–19.8 2.3 (8)	7.9±0.14 7.7–8.4 2.7 (9)	6.2±0.10 5.9–6.4 2.7 (10)	4.9±0.06 4.8–5.1 1.9 (10)	6.9±0.07 6.8–7.1 1.5 (9)	10.1±0.09 10.0–10.4 1.3 (9)
96.0±1.64 86–112 5.5 (42)	12.8±0.14 12–14 3.6 (42)	18.5±0.12 17.7–19.0 1.8 (33)	7.8±0.09 7.4–8.2 3.2 (34)	5.9±0.05 5.5–6.1 2.5 (37)	4.7±0.04 4.4–5.0 3.0 (39)	6.8±0.07 6.2–7.0 2.9 (36)	9.8±0.07 9.3–10.2 2.1 (36)
96.7±1.32 85–104 4.1 (37)	13.0±0.13 12–14 3.1 (37)	18.7±0.17 18.1–19.7 2.2 (22)	7.9±0.08 7.5–8.4 2.6 (29)	6.1±0.10 5.4–6.6 4.2 (28)	5.0±0.05 4.7–5.3 3.0 (30)	6.8±0.08 6.4–7.2 3.2 (30)	10.0±0.10 9.5–10.4 2.2 (20)
105.3±2.54 100–110 3.6 (9)	13.4±0.31 13–14 3.5 (9)	19.7±0.22 19.2–20.2 1.5 (8)	8.4±0.18 8.0–8.6 2.8 (7)	6.7±0.14 6.4–6.8 2.5 (6)	5.1±0.12 4.9–5.3 3.1 (7)	7.4±0.15 7.0–7.6 2.7 (7)	10.5±0.23 10.0–10.7 2.9 (7)
91.7±1.73 83–99 5.6 (35)	12.8±0.29 11–14 6.6 (34)	18.3±0.18 17.5–19.0 2.4 (23)	7.8±0.07 7.4–8.4 2.8 (38)	6.1±0.06 5.5–6.4 2.9 (34)	4.8±0.05 4.5–5.1 3.4 (36)	6.8±0.05 6.4–7.0 2.0 (36)	9.6±0.14 8.8–10.0 3.3 (19)

100.8±1.49 90–110 4.5 (38)	13.5±0.27 11–15 6.1 (38)	<i>C. mexicana peregrina</i> (8), Sierra Madre del Sur, Oaxaca	19.6±0.16 18.6–20.2 2.0 (25)	8.4±0.08 7.8–8.8 2.4 (29)	6.3±0.09 5.7–6.7 3.7 (29)	5.0±0.04 4.6–5.1 2.5 (30)	7.0±0.07 6.6–7.4 2.8 (27)	10.2±0.16 9.7–10.7 3.6 (22)
105.3±2.67 95–117 5.2 (17)	14.5±0.45 12–16 6.4 (17)	<i>C. goldmani alticola</i> (1), eastern Michoacán, Estado de México, and Distrito Federal	20.3±0.33 19.4–21.0 2.6 (10)	8.7±0.20 8.2–9.1 3.9 (12)	6.6±0.11 6.4–7.0 2.9 (12)	5.1±0.06 4.9–5.3 2.3 (13)	7.3±0.12 6.8–7.5 3.0 (13)	10.4±0.12 10.1–10.7 2.1 (13)
106.7±2.63 99–116 4.6 (14)	14.4±0.32 13.5–15.0 4.1 (14)	<i>C. goldmani alticola</i> (2), Jalisco and western Michoacán	20.4±0.18 19.9–21.0 1.5 (12)	8.7±0.12 8.3–9.1 2.5 (13)	6.9±0.15 6.2–7.2 3.9 (12)	5.3±0.07 5.1–5.5 2.3 (12)	7.3±0.12 6.9–7.7 3.0 (13)	10.5±0.12 10.3–11.0 2.0 (12)
101.8±2.60 92–113 5.4 (18)	13.4±0.34 12.0–14.5 5.4 (18)	<i>C. goldmani goldmani</i> (3), Guerrero	19.7±0.24 19.0–20.2 2.1 (12)	8.6±0.14 8.1–9.0 3.2 (15)	6.4±0.09 6.1–6.7 2.9 (16)	5.2±0.12 4.9–5.5 4.4 (16)	7.1±0.07 6.9–7.4 2.0 (15)	10.3±0.16 9.9–11.0 2.8 (13)
104.2±3.08 90–111 5.9 (16)	13.9±0.60 11–15 9.1 (18)	<i>C. goldmani goldmani</i> (4), Oaxaca	19.6±0.42 18.2–20.7 3.7 (12)	8.4±0.19 7.8–8.9 4.5 (15)	6.2±0.10 5.7–6.5 3.3 (16)	5.1±0.11 4.7–5.4 4.2 (16)	7.2±0.13 6.8–7.6 3.4 (15)	10.2±0.21 9.2–10.9 3.9 (15)
105.2±2.45 100–114 3.6 (10)	14.9±0.33 14–16 3.5 (10)	<i>C. goldmani goldmani</i> (5), Chiapas	20.1±0.26 19.4–20.5 1.7 (7)	8.7±0.12 8.4–8.9 1.9 (7)	6.3±0.11 6.2–6.6 2.2 (7)	5.3±0.09 5.1–5.5 2.7 (10)	7.4±0.12 7.1–7.8 2.4 (9)	10.3±0.13 9.2–10.6 1.9 (9)
113.1±2.10 103–128 5.4 (34)	15.3±0.26 14–17 4.8 (33)	<i>C. goldmani goldmani</i> (6), Guatemala	20.1±0.24 19.3–20.5 1.9 (10)	8.6±0.10 8.2–8.8 2.0 (12)	6.2±0.08 6.0–6.4 2.0 (10)	5.3±0.08 5.0–5.5 3.1 (17)	7.4±0.08 7.0–7.6 2.3 (18)	10.3±0.10 10.1–10.8 1.8 (13)
80.3±2.21 76–87 4.1 (9)	15.3±0.26 14–17 4.8 (33)	<i>C. goodmani</i> , Guatemala	21.1±0.23 20.4–21.9 2.3 (18)	9.3±0.10 8.5–9.4 2.6 (24)	7.0±0.09 6.5–7.3 3.0 (24)	5.7±0.07 5.4–6.0 3.0 (25)	7.7±0.11 7.0–8.4 3.6 (25)	11.2±0.15 10.6–11.8 2.9 (19)
11.8±0.27 11–12 3.6 (10)	15.7±0.25 15.0–16.2 2.5 (10)	<i>C. parva herlandi</i> (1), vicinity of Río Grande in Texas and adjacent México	6.4±0.11 6.1–6.6 2.8 (12)	5.2±0.15 4.9–5.7 4.8 (12)	3.6±0.08 3.5–4.0 3.8 (12)	5.7±0.09 5.5–5.9 2.6 (12)	8.0±0.26 7.7–8.4 3.6 (5)	

Table 1.—Continued.

Total length	Length of hind foot	Condylar basal length	Palatal length	Maxillary breadth	Interorbital breadth	Maxillary toothrow	Cranial breadth
75.4±2.15 69-86 6.2 (19)	10.9±0.27 10-12 5.3	16.0±0.26 15.3-16.9 3.0 (14)	C. <i>parva berlandieri</i> (2), southern Tamaulipas and San Luis Potosí 6.7±0.13 6.2-7.3 4.3 (19)	5.1±0.08 4.7-5.3 3.4 (17)	3.7±0.07 3.4-3.9 3.8 (19)	5.8±0.14 5.2-6.3 5.3 (19)	7.9±0.14 7.5-8.3 3.2 (13)
79.0±1.99 70-87 6.0 (23)	11.1±0.34 10-12 7.5 (24)	16.4±0.19 15.5-17.1 2.7 (23)	C. <i>parva berlandieri</i> (3), Nayarit, Jalisco, Guanajuato, and Michoacán 6.8±0.05 6.3-7.3 3.2 (72)	5.1±0.04 4.9-5.7 3.0 (66)	3.7±0.05 3.3-4.1 5.1 (72)	5.7±0.06 5.4-6.2 3.0 (33)	8.1±0.09 7.7-8.5 2.6 (22)
78.3 76-80 (3)	10.7±0.60 10.0-11.5 6.3 (5)	16.8 16.4-17.4 (3)	C. <i>parva orophila</i> (10), Honduras, El Salvador, and Nicaragua 7.1 6.8-7.5 (4)	5.4 5.1-5.6 (4)	3.9 3.7-4.3 (4)	6.1±0.13 5.8-6.4 3.7 (5)	8.4 8.4-8.5 (2)
84.7±3.60 77-93 6.7 (10)	11.6±0.50 10-13 7.9 (13)	16.3±0.42 15.4-16.9 3.2 (6)	C. <i>parva orophila</i> (11), Costa Rica and Panamá 7.1±0.31 6.2-8.0 7.0 (10)	5.4±0.12 5.9-5.6 3.5 (9)	4.0±0.16 3.7-4.3 5.6 (8)	6.2±0.13 5.9-6.7 3.9 (15)	8.2 8.1-8.3 (3)
84.7±2.78 77-92 5.5 (11)	11.8±0.63 10-13 9.2 (12)	16.5±0.49 16.1-17.4 3.6 (6)	C. <i>parva pueblensis</i> (5), southern San Luis Potosí, northern Veracruz, and Puebla 6.9±0.13 6.6-7.3 3.2 (12)	5.2±0.11 4.9-5.5 3.8 (13)	3.9±0.12 3.7-4.3 4.7 (10)	6.2±0.10 5.9-6.5 2.6 (11)	8.2±0.22 7.8-8.8 3.7 (8)
84.3±1.68 73-92 5.2 (27)	11.9±0.22 11-13 4.8 (27)	16.8±0.17 15.9-17.5 2.4 (22)	C. <i>parva pueblensis</i> (6), southern Veracruz 7.0±0.07 6.5-7.4 2.7 (29)	5.3±0.09 4.7-5.8 4.2 (28)	3.9±0.06 3.5-4.2 4.1 (27)	6.2±0.06 5.8-6.5 2.7 (30)	8.3±0.10 7.6-8.6 3.0 (25)
89.3±3.03 74-99 7.2 (18)	12.0±0.35 11-13 6.5 (20)	17.1±0.22 16.6-17.8 2.1 (11)	C. <i>parva pueblensis</i> (7), Oaxaca 7.2±0.12 6.9-7.7 3.3 (16)	5.6±0.11 5.3-6.0 4.1 (17)	4.2±0.10 3.9-4.6 4.8 (17)	6.2±0.14 5.8-6.8 4.8 (18)	8.5±0.18 8.1-8.9 3.3 (10)
85.9±2.52 81-90 6.1 (18)	11.6±0.69 10-13 8.5 (8)	17.4±0.37 16.4-18.4 3.2 (9)	C. <i>parva pueblensis</i> (8), Chiapas 7.0±0.11 6.1-7.7 4.3 (29)	5.6±0.09 5.2-6.0 4.0 (26)	4.3±0.06 3.8-4.7 4.1 (30)	6.1±0.09 5.7-6.8 3.9 (29)	8.4±0.28 8.1-8.9 4.1 (6)

		<i>C. parva soricina</i> (4), Valley of Mexico				<i>C. parva soricina</i> (4), Valley of Mexico			
90.0 88-92	(2)	12.2 12.0-12.5	16.9±0.27 16.6-17.2	6.9±0.06 6.6-7.3	5.2±0.18 5.0-5.5	3.9±0.24 3.6-4.2	6.2 6.1-6.2	8.1 7.4-8.5	
93.6±4.10 85-103	(3)	12.5±0.38 12-13	17.8±0.29 17.3-18.1	7.5±0.18 7.1-7.7	5.8±0.13 5.5-6.0	4.1±0.12 4.0-4.3	6.6±0.08 6.4-6.7	8.8 8.4-8.9	
6.2 (8)	4.3	12.1±0.43 11-13	18.7±0.52 17.8-19.4	7.9±0.28 7.2-8.7	6.1±0.15 5.6-6.6	4.4±0.12 4.1-4.8	6.9±0.24 6.1-7.4	9.1±0.35 8.3-9.6	
5.9 (9)	5.6	13.0±0.67 11-14	19.4±0.31 18.8-19.8	8.5±0.29 8.0-9.7	6.4±0.09 6.2-6.6	4.8±0.15 4.3-5.1	6.3 6.3 (13)	5.1 5.1 (7)	
7.4 (9)	7.7	11.5±0.28 10.5-12.0	18.4±0.28 17.8-19.4	7.8±0.13 7.3-8.4	6.1±0.15 5.7-6.6	4.8±0.15 4.2-4.9	7.2±0.18 6.7-7.7	9.8±0.38 9.3-10.4	
5.5 (7)	4.9	12.1±0.47 11-13	18.2 17.9-18.4	7.6 7.5-7.8	6.1 6.0-6.3	4.7 4.6-4.8	6.8 6.6-7.2	4.4 3.8 (5)	
3.3 (7)	5.2	13.9±0.19 13-15	19.6±0.19 18.6-20.7	8.5±0.12 7.8-9.1	5.8±0.08 5.4-6.2	4.8±0.09 4.1-5.2	7.2±0.07 6.8-7.7	9.8±0.11 9.1-10.3	
6.8 (35)	4.0	16.7±0.36 16.0-17.5	23.1±0.26 22.5-23.7	9.9±0.20 9.5-10.6	7.5±0.09 7.3-7.8	5.6±0.06 5.4-5.7	8.6±0.15 8.2-9.0	11.8±0.17 11.4-12.4	
3.9 (10)	3.6	12.7±2.43 12.3-13.5	16.7±0.36 16.0-17.5	23.1±0.26 22.5-23.7	9.9±0.20 9.5-10.6	7.5±0.09 7.3-7.8	5.6±0.06 5.4-5.7	8.6±0.15 8.2-9.0	

is to adult summer pelage or adult winter pelage. Molt from juvenal pelage to winter pelage begins on the venter or above the rump, usually progresses more rapidly on the venter than on the dorsum, frequently forms a "saddle" across the back, and progresses anteriorly so that the top of the head is the last area on which molt is completed. Molt from juvenal to summer pelage is not so regular; sometimes it begins anteriorly and progresses posteriorly, but occasionally the reverse pattern (as in molt from juvenal pelage to winter pelage) occurs. Autumnal molt of adults follows the same pattern as post-juvenal molt to winter pelage. Spring molt, on the other hand, usually begins on the head and progresses ventrally and posteriorly so that the rump is the last area to molt, but a few specimens exhibit the reverse pattern. The overall pattern of molt, therefore, is as follows: the autumnal molt, irrespective of age, takes place according to a relatively fixed pattern (roughly from posterior to anterior), whereas the spring molt, whether from winter pelage to summer pelage or from juvenal pelage to summer pelage, is irregular (although most often proceeding from anterior to posterior). Complicating the matter is the fact that old adults (second year animals) molt erratically in that molt can begin at almost any time of the year, frequently stops before completion, and produces complicated patterns of old, new, and incoming hair. Probably the endocrinial or other physiological mechanisms that contribute to regulation of molt have ceased to function properly during the second year of life in these individuals.

In most species of *Cryptotis*, juvenal pelage differs from adult pelage in being darker, grayer, and in having a "fuzzy" appearance. Also, juvenal pelage frequently lacks the basal gray region characteristic of adult pelage. There is some evidence that in at least a few taxa the first post-juvenal pelage averages darker than subsequent pelages; that is, the pelage of a young (first year) adult tends to be darker than that of an old (second year) adult in the same season. There is not sufficient differentiation, however, to justify recognition of the first post-juvenal pelage as a distinct subadult pelage, especially since it conforms to the molt schedule of adult pelages.

Seasonal regulation of molt exists in all species of *Cryptotis*, but it is not presently known whether schedules of molt in Middle American kinds conform more directly to temperate seasons (summer and winter) or to tropical seasons (wet and dry). The distribution of *Cryptotis* in tropical America, however, is most extensive within temperate ecological zones, supporting retention of classical terminology for seasonal pelages.

Winter pelage generally is longer and browner than summer pelage, but the degree of difference varies from species to species and from population to population within species. Seasonal differentiation of pelages is most pronounced in regions that experience pronounced climatic seasonality. Therefore, winter pelage is markedly longer and more luxuriant than summer pelage in *C. goldmani*, which occurs at high elevations where winter snow is frequent, whereas the distinction is slight in *C. mexicana*, which occurs in a relatively constant micro-environment on the floor of cloud forests. Failure of some previous workers to distinguish between winter and summer pelages in *Cryptotis* has resulted in taxonomic confusion; for example, specimens of *C. goldmani* collected in winter were named as one species and those taken in summer as another.

KEY TO RECENT MIDDLE AMERICAN SPECIES OF CRYPTOTIS

1. Tail elongate, more than 45 per cent of length of head and body; rostrum elongate; postcentrocrista and metacone usually present on M3, metacrista sometimes present; entoconid present on m3.
 2. Dentition bulbous; posterior surfaces of P4-M2 never recessed: broad.
 3. Size large (total length 123-135; condylobasal length 22.5-23.7); occurs only in southern México *C. magna*, p. 287
 - 3'. Size medium (total length 109; condylobasal length 20.4); occurs only in southern Central America *C. endersi*, p. 285
 - 2'. Dentition not bulbous; posterior surfaces of P4-M2 sometimes slightly recessed; rostrum slender *C. gracilis*, p. 281
- 1'. Tail not elongate, less than 45 per cent of length of head and body; rostrum not markedly elongate; postcentrocrista, metacone, and metacrista usually reduced or lacking on M3; entoconid reduced or lacking on m3 in certain taxa.
 4. Dentition bulbous *C. nigrescens*, p. 270
 - 4'. Dentition not bulbous.
 5. Front feet enlarged; claws conspicuously long and broad.
 6. Size large (total length 103-128; condylobasal length 20.4-21.9; cranial breadth 10.6-11.8); talonid of m3 reduced, consisting only of hypoconid, and shortened antero-posteriorly; winter pelage usually almost black; upper surfaces of feet usually black *C. goodwini*, p. 249
 - 6'. Size medium to large (total length in region of potential geographic sympatry with *goodwini* 101-111; condylobasal length 19.3-20.5; cranial breadth 10.1-10.8); talonid of m3 only moderately reduced, usually consisting only of hypoconid but rudimentary entoconid sometimes present, not shortened antero-posteriorly; winter pelage dark brown, usually with slight olive cast, upper surfaces of feet usually pale *C. goldmani*, p. 239

5'. Front feet small; claws short and slender.

7. Size medium (total length 83-112; condylobasal length 17.5-20.2); talonid of m3 almost always consisting of both hypoconid and well-developed entoconid; posterior surfaces of P4-M2 only slightly if at all recessed; color of venter usually dark, only slightly paler than dorsum *C. mexicana*, p. 224

7'. Size small (total length in region of geographic sympatry with *mexicana* 69-99; condylobasal length 15.3-18.4); talonid of m3 consisting only of hypoconid; posterior surfaces of P4-M2 moderately to considerably recessed; color of venter whitish, considerably paler than dorsum *C. parva*, p. 251

RECENT MIDDLE AMERICAN SPECIES OF CRYPTOTIS

Cryptotis mexicana-group

Cryptotis mexicana

(Synonymy under subspecies)

Distribution.—Sierra Madre Oriental from at least as far north as Gómez Farías, Tamaulipas, southward through northeastern Querétaro, Hidalgo, and northern Puebla to west-central Veracruz, with an isolated population on the Sierra de los Tuxtlas in southern Veracruz, thence southward on the Sistema Montañoso and the Sierra Madre del Sur in Oaxaca, and eastward across the Isthmus of Tehuantepec to the Mesa Central of Chiapas (Fig. 6).

Diagnosis.—External characteristics: size medium for the genus (Table 1); tail relatively short, averaging 33-42 per cent of length of head and body; front feet and claws not enlarged; juvenal and adult summer pelages seldom distinctively colored, blackish gray because of shortness of reddish brown tips on otherwise gray hairs; winter pelage luxuriant and vermiculations present only when pelage is fresh (and even then primarily at higher elevations), dorsum dark brown, varying from Sepia or Clove to Bister or Mummy Brown in old specimens (1894), near Bister or Clove in recently taken specimens (1964); overall appearance of venter usually only slightly paler than dorsum, although individual hairs tipped with pale buff.

Cranial characteristics: rostrum relatively short; braincase angular; anterior limit of zygomatic plate varying from slightly anterior to metastyle of M1 to above juncture of M1 and M2; posterior limit of zygomatic plate at level of or posterior to maxillary process, above M3; dentition not bulbous; anterior element of ectoloph of M1 not reduced relative to posterior element; posterior surfaces of P4-M2 negligibly or only slightly recessed; protoconal basin of M1 not reduced relative to hypoconal basin; M3 consisting of paracrista, precentrocrista, postcentrocrista, and metacone (vestigial metacrista, hypocone, or cingular cusplet sometimes present); talonid of m3 consisting of well-developed hypoconid and entoconid, the latter infrequently reduced.

Comparisons.—Comparisons with *C. goldmani*, *C. magna*, *C. nigrescens*, and *C. gracilis* are given in the accounts of those species.

From *C. goodwini*, *C. mexicana* differs as follows: size smaller, both externally and cranially (although the extremes of some measurements of *goodwini* overlap those of the geographically distant subspecies *C. m. nelsoni* and *C. m. peregrina*—Table 1); front feet and claws conspicuously smaller; pelage darker,

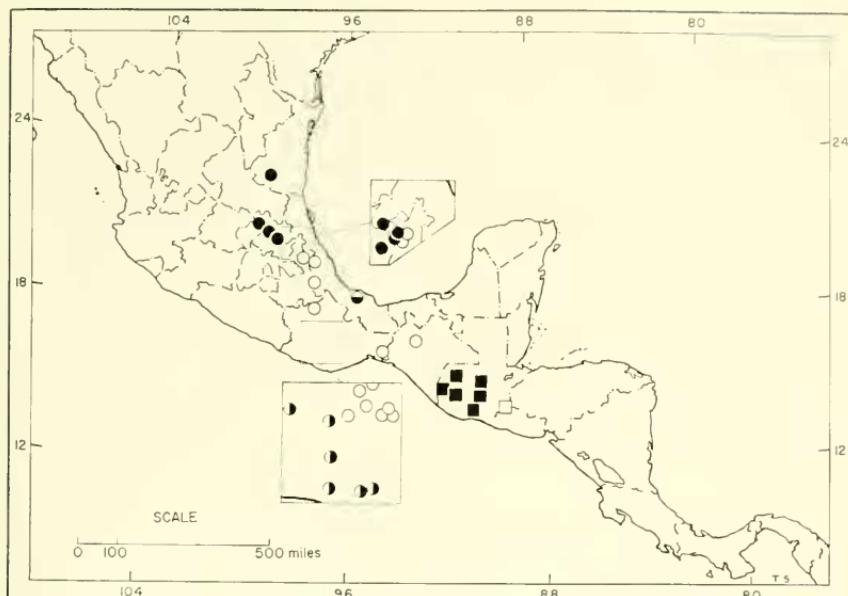


FIG. 6. Geographic distribution of *Cryptotis mexicana* and *C. goodwini*. Solid circles, *C. mexicana obscura*; open circles, *C. mexicana mexicana*; circle solid below, *C. mexicana nelsoni*; circles solid right, *C. mexicana peregrina*; solid squares, *C. goodwini*; open square, literature record for *C. goodwini*.

less luxuriant; anterior element of ectoloph of M1 not reduced relative to posterior element, as opposed to reduced; posterior surfaces of P4-M2 only slightly or not at all recessed, as opposed to considerably recessed; protoconal basin of M1 not reduced relative to hypoconal basin, as opposed to reduced; metacone and postcentrocrista usually present on M3, as opposed to seldom present.

From *C. parva*, *C. mexicana* differs as follows: size conspicuously larger, both externally and cranially (Table 1); pelage darker, never whitish ventrally; zygomatic plate situated farther posteriorly; anterior element of ectoloph not reduced relative to posterior element; posterior surfaces of P4-M2 only slightly or not at all recessed, as opposed to considerably recessed in *parva*; protoconal basin of M1 not reduced relative to hypoconal basin; metacone and precentrocrista usually present on M3 (seldom present in *parva*); talonid of m3 consisting of both hypoconid and entoconid (reduced and consisting only of entoconid in *parva*).

From *C. endersi*, *C. mexicana* differs as follows: tail relatively and actually shorter, averaging 29-36 (as opposed to 49) per cent of length of head and body; rostrum relatively and actually much less elongate; braincase more angular; dentition not bulbous.

Remarks.—Authorship of the name "*Blarina (Soriciscus) mexicana*" (and names of certain other shrews) has been attributed to Spencer F. Baird by several workers who adhered to the expressed intention of Elliott Coues (1877:631) to honor Baird as the authority for names proposed formally by Coues. Merriam (1895) also listed Baird as the authority for *mexicana*, but his revision was published

prior to establishment of the International Rules of Zoological Nomenclature. Most authors—including Miller (1912), Miller (1924), Jackson (1928), Miller and Kellogg (1955), and Hall and Kelson (1959)—of taxonomic papers and compilations published subsequent to formal adoption of standardized rules of nomenclature have recognized Coues as the authority for *mexicana* (and the other names in question). Article 50 of the International Code of Zoological Nomenclature, as adopted in 1961 at the Fifteenth International Congress of Zoology, permits a person other than the author of the paper in which a name is proposed to be recognized as the author of that name only if he “is alone responsible both for the name and the conditions that make it available.” Coues admittedly contributed to the description of *mexicana* and therefore must be recognized as authority.

In his lists of specimens in the British Museum, Gray (1843:xxi; 1847:xi, 23) listed the “Mexican shrew,” “*Blaria Mexicana*,” from “Coban, South America” [Cobán, Guatemala]. As pointed out by Merriam (1895:23), this name is a *nomen nudum*.

The name “*mexicana*” has been applied, in one sense or another, to almost all of the large Middle American representatives of the genus *Cryptotis*. Merriam (1895) was the first to attempt a detailed treatment of geographic variation in *C. mexicana*, but he understandably confused *C. mexicana* with the closely related *C. goldmani*, and perpetuated the confusion by describing and naming two populations of *C. goldmani* as subspecies (*goldmani* and *machetes*) of *C. mexicana*. Subsequent workers resorted to liberal use of the term “*mexicana*-group” as a catch-all category for Middle American taxa herein referred to that group as well as several that are referred to other groups. Fifteen different specific and subspecific names (see synonymies of *C. goodwini* and of subspecies of *C. mexicana* and *C. goldmani*) have been applied to representatives herein classified in the *mexicana*-group. These resulted from the efforts of several researchers (Coues, 1877; Merriam, 1895; Miller, 1911; Jackson, 1933; Goodwin, 1954a; Schaldach, 1966; Genoways and Choate, 1967) to elucidate variation. However, by placing emphasis on differences (thereby shrouding similarities), they served inadvertently to retard a biological understanding of the group.

Cryptotis mexicana is the most generalized representative of the *mexicana*-group, retaining more primitive morphological features than either *C. goldmani* or *C. goodwini*. It would be possible to derive the dental patterns in each of those species from the pattern in Recent *mexicana* by processes of reduction: emargination of pos-

terior surfaces of P4-M2; reduction and eventual loss of cristae and cusps on M3; and reduction and eventual loss of the entoconid on m3, followed by shortening of the talonid. Other external and cranial characteristics by which *goldmani* and *goodwini* differ from *mexicana* also are regarded as specializations. It seems likely, therefore, that *mexicana* was the precursor of both *goldmani* and *goodwini*; a zoogeographic interpretation of the events that may have resulted in this diversity is presented in a later section of this paper.

Cryptotis mexicana is polytypic, consisting of four well-differentiated subspecies that do not vary markedly in color but differ significantly in size. One of the subspecies (*nelsoni*) is isolated by a distance of at least 75 miles from the nearest area that is likely to be inhabited by other populations of the species at this time; gene flow among other subspecies apparently is continuous through narrow zones of intergradation.

The distribution of *mexicana* is restricted primarily to humid montane forests in eastern and southern México. Elevations at which representatives of the species have been obtained vary as follows: 3500-4400 feet on the Sierra Madre Oriental in Tamaulipas (see also Alvarez, 1963:396-397); 5500-9500 feet in Querétaro; 3700-9500 feet in Hidalgo; 4300-5000 feet in Puebla; 1700-8500 feet in Veracruz; 4800 feet on Volcán San Martín in Veracruz; 3100-10,500 feet on the Sistema Montañoso and 4200-9500 feet on the Sierra Madre del Sur in Oaxaca; and 7000 feet on the Mesa Central in Chiapas. Most specimens for which field notes are available were collected in cloud forests of oak or pine, or pine mixed with oak, frequently interspersed with abundant mosses, lichens, orchids, and bromeliads. In terms of biotic assemblages, *C. mexicana* resides primarily in the Humid Upper Tropical Subzone of Goldman (1951:346-352), with some overlap into the Canadian Zone. Published accounts, such as that of Hall and Dalquest (1963:206), seem also to indicate local abundance of the species in some humid tropical habitats other than undisturbed forests.

Specimens of *mexicana* judged to be young (unworn teeth, juvenal pelage) are available from every month of the year. Likewise, subadults, adults, and old adults are represented in almost every month. It would appear, therefore, that *mexicana* reproduces throughout the year, at least when all populations of the species from various elevations and latitudes are considered together. The portions of the year spent, respectively, in summer and winter pelage vary geographically and altitudinally, as do the times of molting. Individuals in summer pelage have been collected in May through

December; those molting from summer to winter pelage in September and October; those molting from juvenal to winter pelage in December and January; those in winter pelage in September, and December through April; those molting from winter to summer pelage in June; and those individuals molting from juvenal to summer pelage in May, and July through October.

Geographic variation.—Size in *C. mexicana*, with few exceptions, varies clinally from northwest (smaller) to southeast (larger). Geographic variation in total length demonstrates the cline as well as the exceptions (refer to Methods and Materials for a listing of localities included in each numbered sample). Specimens from the northern part of the range on the Sierra Madre Oriental (sample 1) have a significantly smaller mean total length than those from other parts of the range. Total length does not differ significantly among other samples (2, 4, 6, and 7) on the Sierra Madre Oriental and the Sistema Montañoso in Hidalgo, Puebla, Veracruz, or Oaxaca except in the vicinity of Las Vigas, Veracruz (sample 3), where individuals average significantly larger than those from areas farther to the south. The mean total length of specimens from the Sierra Madre del Sur in Oaxaca (sample 8) is substantially larger than that of shrews from all other populations except those inhabiting the Sierra de los Tuxtlas in Veracruz (sample 5), which are the largest representatives of *C. mexicana*.

Length of tail is not so variable with respect to latitude as is total length. Specimens from the northern part of the Sierra Madre Oriental (sample 1) do not differ significantly from those from most localities farther to the south, but have a significantly shorter mean length of tail than specimens from the geographically contiguous population in the vicinity of Huauchinango, Puebla (sample 2). The tail averages longest in populations on the Sierra de los Tuxtlas in Veracruz (sample 5) and the Sierra Madre del Sur in Oaxaca (sample 8).

Individuals from the northern limit of the range (sample 1) average significantly smaller in length of hind foot than those from the central region (samples 2 and 3) of the distribution on the Sierra Madre Oriental, but do not differ significantly from individuals representing populations (samples 4, 6, and 7) at the southeastern end of the distribution of the species. Again, specimens from the Sierra de los Tuxtlas (sample 5) and the Sierra Madre del Sur (sample 8) do not fit into a clinal pattern of variation, being at or near the upper limit of variation in size.

Condyllobasal length, palatal length, and cranial breadth exhibit

almost identical patterns of variation. As with other measurements, specimens from the Gómez Farías region of Tamaulipas southward to northern Puebla (sample 1) are significantly smaller than those from adjacent populations in the vicinities of Huauchinango, Puebla (sample 2), and Las Vigas, Veracruz (sample 3), but do not differ significantly from specimens from populations on the Sistema Montañoso in Oaxaca (samples 6 and 7). The skull and palate average longest, and the cranium broadest, in populations inhabiting the Sierra de los Tuxtlas (sample 5) and the Sierra Madre del Sur (sample 8).

Maxillary breadth and interorbital breadth exhibit similar, although not identical, patterns of variation. Specimens from southern Tamaulipas, northeastern Querétaro, Hidalgo, and northern Puebla (sample 1) and from populations on the northern part of the Sistema Montañoso in Oaxaca (sample 6) have the narrowest rostra, whereas specimens from intervening localities generally increase in size from south to north. The rostrum averages significantly broader in specimens from the Sierra de los Tuxtlas in Veracruz (sample 5) than in any other population sampled. Specimens from the Tuxtlas also have larger means for length of maxillary toothrow and length of M2 than specimens from other populations.

Certain external, cranial, and dental qualitative characteristics also vary geographically in *C. mexicana*, but were not tested statistically. In general, dental configuration is a conservative character with respect to geography; the only major deviations from the primitive *mexicana* pattern occur in populations inhabiting the Sierra Madre del Sur in Oaxaca. In that part of the range there is a pronounced tendency for dental configurations to be intermediate between those characteristic of *C. mexicana* and *C. goldmani*, as well as apparent genetic or developmental instability regarding formation or development of the fourth upper pair of unicuspids. Likewise, the third upper and lower molars tend to be reduced, the lowers frequently having vestigial entoconids, and the upper molariform teeth tend to be slightly recessed posteriorly. Variation as to presence or absence of one or the other, or both, of the fourth upper unicuspids apparently is most pronounced in populations inhabiting the coastal range of the Sierra Madre del Sur in southern Oaxaca, but occurs to a lesser extent in other parts of the Sierra Madre of that state.

The only other dental characteristic that seemingly varies geographically is extent of pigmentation. The teeth of individuals from populations in Tamaulipas, Querétaro, Hidalgo, and Puebla are

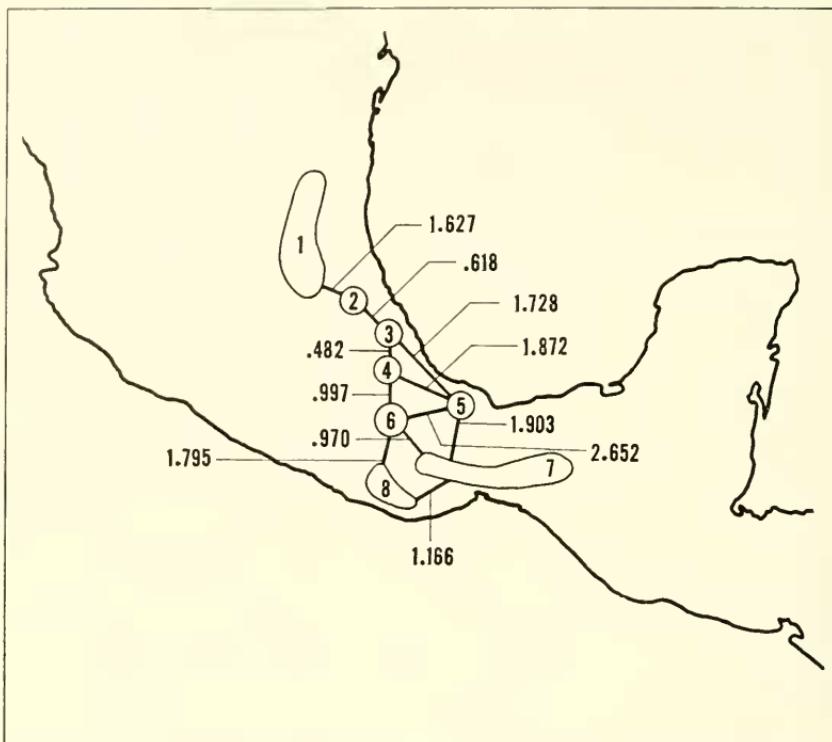


FIG. 7. Semi-diagrammatic representation of geographic relationships of samples of *Cryptotis mexicana*. Localities included in numbered samples are listed in Methods and Materials. Distance coefficients are illustrated for all potential routes of gene flow; the lower the coefficient, the greater the resemblance (see text).

pigmented with a darker color (sometimes almost black rather than the usual mahogany) than are those of individuals from populations farther to the south. There are no readily apparent geographic trends in color of pelage, though slight local variation is common.

Front feet and claws demonstrate a pronounced tendency to be larger and more highly developed for semi-fossorial habits in populations inhabiting the Sierra Madre del Sur in Oaxaca than in populations from other parts of the range. Even so, the feet and claws in *mexicana* never approach the extent of development characteristic of populations of *C. goldmani*, with which *mexicana* is sympatric in Oaxaca.

Distance coefficients for all mensural characters considered together are shown in Fig. 7. Only those routes of gene flow that are feasible when distribution of suitable habitat is taken into consideration are illustrated. Sample 1, from northeastern México, is set off

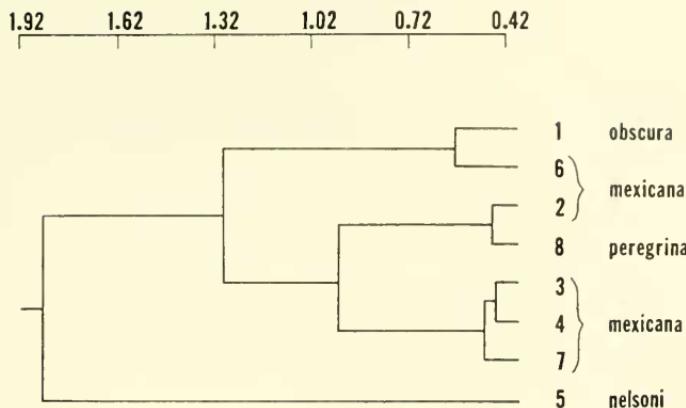


FIG. 8. Phenogram of numbered samples (see Fig. 7) of *Cryptotis mexicana* computed from distance matrices on standardized characters and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram is 0.794. Subspecific assignment is indicated to the right of the sample numbers.

from sample 2, from the vicinity of Huauchinango, Puebla, and adjacent Hidalgo, by a distance coefficient of 1.627, and is considered to represent a distinct subspecies (*obscura*). Sample 5, from the Sierra de los Tuxtlas, Veracruz, is separated from other populations with which intergradation is geographically feasible by distance coefficients of 1.728, 1.872, 2.652, and 1.903, and is considered to represent a second well-differentiated subspecies (*nelsoni*). Sample 8, from the Sierra Madre del Sur in Oaxaca, is set off from samples 6 and 7, from the Sistema Montañoso in Oaxaca, by distance coefficients of 1.795 and 1.166, respectively, and is considered to represent a third subspecies (*peregrina*). Samples 2, 3, 4, 6, and 7, from the southern part of the Sierra Madre Oriental and the Sistema Montañoso, are separated from one another by small distance coefficients relative to those previously mentioned, and are construed to represent a single wide-ranging subspecies (*mexicana*).

A reasonable argument could be made for splitting the nominate subspecies into two or three additional subspecies on the basis of disparities in magnitude of distance coefficients. Indeed, a phenogram (Fig. 8) computed from distance matrices divided the nominate subspecies into two geographically meaningless groups separated by *peregrina*. However, recognition of only four subspecies is supported by individual analyses of single mensural characters, by multivariate analyses, and by geographic variation of qualitative external and

dental characters, and is explicable in terms of geographic and topographic features. Furthermore, the subspecies of *C. mexicana* as here recognized differ sufficiently in size from one another to permit relatively simple assignment of individual specimens to one or another taxon without reference to locality of capture.

***Cryptotis mexicana mexicana* (Coues)**

Blarina (Soriciscus) mexicana Cones, Bull. U.S. Geol. and Geog. Surv. Territories, 3:652, 15 May 1877 [not *Blaria Mexicana* Gray, List of the specimens of Mammalia in the collection of the British Museum, p. xxi, 1843, from Cobán, Guatemala, a *nomen nudum*].

Cryptotis mexicana, Miller, Proc. Biol. Soc. Washington, 24:221, 31 October 1911.

Blarina mexicana, Alston, Biologia Centrali-Americana, Mammalia, p. 57, February 1880; True, Proc. U.S. Nat. Mus., 7:606, 29 November 1884; Merriam, N. Amer. Fauna, 10:24, 31 December 1895.

Cryptotis mexicana mexicana, Miller, Bull. U.S. Nat. Mus., 79:26, 31 December 1912; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959; Hall and Dalquest, Univ. Kansas Publ., Mus. Nat. Hist., 14:205, 20 May 1963; Genoways and Choate, Proc. Biol. Soc. Washington, 80:204, 1 December 1967; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:39, 30 April 1969 (*part*).

Cryptotis mexicana peregrina, Goodwin, Bull. Amer. Mus. Nat. Hist., 141:39, 30 April 1969 (*part*).

Holotype.—Young, sex unknown, skin (juvenile pelage) and skull, U.S. National Museum no. 3525/4438, obtained by R. Montes de Oca on an unknown date (skin catalogued on 18 March 1859, skull in September 1861); type locality, Jalapa, *ca.* 5000 ft., Veracruz.

Distribution.—Sierra Madre Oriental from east-central Hidalgo and northern Puebla southward throughout west-central Veracruz and probably adjacent Puebla, southeastward in Oaxaca on the Sistema Montañoso, thence across the Isthmus of Tehuantepec and onto the Mesa Central in Chiapas (Fig. 6).

Measurements of holotype.—Palatal length 7.8; interorbital breadth 5.0; length of maxillary toothrow 6.9; length of M2 1.5.

Comparisons.—From *C. m. obscura*, *C. m. mexicana* differs in having slightly less reddish pelage, less darkly pigmented teeth, and significantly larger external and cranial dimensions (Table 1). From *C. m. nelsoni*, *C. m. mexicana* differs in having slightly paler pelage and significantly smaller external and cranial dimensions (Table 1). From *C. m. peregrina*, *C. m. mexicana* differs in having less highly developed front feet and claws, darker ventral coloration, and significantly smaller external and cranial dimensions (Table 1).

Remarks.—Morphological features of *C. m. mexicana* probably are not far removed from those of the ancestral population of *C. mexicana* that gave rise to *C. goldmani* and *C. goodwini*. Furthermore, characteristics by which the three other recognized subspecies

of *C. mexicana* can be distinguished from *C. m. mexicana* are regarded as specializations from the primitive morphotype of the species. The geographic range of *C. m. mexicana* is centrally located with respect to the other subspecies, and is contiguous, at least potentially, with the ranges of each; to the north is the smaller *C. m. obscura*, and to the east and southwest are the larger *C. m. nelsoni* and *C. m. peregrina*, respectively. Within the range of *C. m. mexicana*, populations in the northwest (in the vicinities of Las Vigas, Veracruz, and Huauchinango, Puebla, and adjacent Hidalgo) average larger, both externally and cranially, than populations in the southeast (on Cerro San Felipe and Cerro Zempoaltepec, Oaxaca—see Table 1). As a result, external and cranial measurements of southern populations of *mexicana* are practically indistinguishable from those of *obscura*, whereas measurements of northwestern populations of *mexicana* approach those of *nelsoni* and *peregrina*. Populations of *mexicana* and each of the other subspecies are, however, clearly distinct. This arrangement of an inverse subcline (representing geographic variation among populations of the subspecies *C. m. mexicana*) within the overall step-cline (representing geographic variation among subspecies of the species) permits easy allocation of specimens to subspecies, at least judging by specimens presently at hand. That the observed mensural displacement between adjacent subspecies is not indicative, instead, of selective interaction between closely related species is shown by the fact that trends in variation of cranial and dental characters are not altered from one population to the next, and intergradation of those characters is associated at least in part with geographic zones of potential or actual intergradation of mensural characters. Comments on intergradation of *C. m. mexicana* with other subspecies are given in accounts of those subspecies.

A single specimen (KU 83942) deserves mention because it is the only specimen referable to *C. mexicana* known from east of the Isthmus of Tehuantepec. It was caught in second-growth cloud forest at a place three miles east of Pueblo Nuevo Solistahuacán, 7000 feet, on the Mesa Central of northern Chiapas. The specimen is a young with relatively small external measurements and almost coal black juvenal pelage, but does not differ noticeably from young individuals of *C. m. mexicana* from Totontepec or elsewhere on the Sistema Montañoso in Oaxaca, and thus is referred to that subspecies. Another specimen (CAS 14636), which was caught on the Isthmus of Tehuantepec near the border of Oaxaca and Chiapas at

a place 8 km. NW "Colonia Rudolfo Figueroa," also is referred to *C. m. mexicana*.

Goodwin (1969:39-42) assigned specimens from Cerro San Felipe, Oaxaca, to both *C. m. mexicana* and *C. m. peregrina*, but I have assigned all of these specimens to *C. m. mexicana*. The specimen from La Muralla, Oaxaca, that was assigned by Goodwin (*op. cit.*:39) to *C. m. mexicana* is transferred to *C. m. peregrina*. It should be pointed out further that the scale of magnification for shrews shown on plates two and three (Goodwin, *op. cit.*) is not consistently accurate; the extent of enlargement of photographs of *C. m. mexicana* and *C. m. peregrina* is less than for some other taxa, thus accounting, for example, for the disparity in cranial size on the plates between *C. m. peregrina* and *Notiosorex phillipsii* Schaldach.

Specimens examined.—219, as follows: VERACRUZ: 4 km. W Tlapacoyan, 1700 ft., 3 (KU); Jalacingo, ca. 6000 ft., 1 (UMMZ); 11 km. W Las Vigas, 8500 ft., 1 (KU); Las Vigas, 8500 ft., 50 (48 KU, 2 USNM); La Joya, 6600 ft., 2 (1 UMMZ, 1 UNAM); 2.6 mi. W Banderilla, ca. 5000 ft., 1 (UMMZ); Jalapa, 5000 ft., 1 (USNM); Xico, 4800-6500 ft., 30 (2 BMNH, 28 USNM); Teocelo, 5000 ft., 3 (MCZ); Huatusco, 5000 ft., 3 (KU); Coscomatepec, 5000 ft., 3 (KU); Orizaba, 4000-4200 ft., 9 (1 BMNH, 8 USNM). HIDALGO: Tenango de Doria, 5200 ft., 2 (UMMZ). PUEBLA: 6 km. N Villa Juárez, 1 (ENCB); Huachinango, 5000 ft., 19 (1 UMMZ, 18 USNM); Xocoyolo, 4300 ft., 2 (UMMZ); 2 mi. NW Zacapoaxtla, 4900 ft., 2 (UMMZ). OAXACA: Teotitlán del Camino, above 3100 ft., 1 (AMNH); Papalo Santos Reyes, 6700-10,200 ft., 13 (USNM); Vista Hermosa, ca. 4900 ft., 1 (KU); Llano de las Flores, 9200-10,300 ft., 6 (1 KU, 5 UMMZ); 7 mi. N Ixtlán de Juárez, 10,000 ft., 2 (CAS); Totontepec, ca. 6000 ft., 9 (USNM); Cerro San Felipe, 10,000-10,300 ft., 26 (3 AMNH, 1 KU, 22 USNM); near San Pedro Cajonos, 8000 ft., 2 (USNM); Cerro Zempoaltepec, 8000-10,500 ft., 24 (USNM); 8 km. NW "Colonia Rudolfo Figueroa" (not exactly located), 5500 ft., 1 (CAS). CHIAPAS: 3 mi. E Pueblo Nuevo Solistahuacán, 7000 ft., 1 (KU).

Cryptotis mexicana nelsoni (Merriam)

Blarina nelsoni Merriam, N. Amer. Fauna, 10:26, 31 December 1895.

Cryptotis nelsoni, Miller, Bull. U. S. Nat. Mus., 79:27, 31 December 1912; Hall and Kelson, The mammals of North America, 1:61, 31 March 1959; Hall and Daubenton, Univ. Kansas Publ., Mus. Nat. Hist., 14:206, 20 May 1963.

Holotype.—Subadult female, skin (adult summer pelage) and skull, U.S. National Museum no. 65437, obtained on 13 May 1894 by E. W. Nelson and E. A. Goldman, original number 6253; type locality, Volcán San Martín, 4800 ft., Veracruz.

Distribution.—Known only from the type locality (Fig. 6); probably occurs in suitable habitats throughout the Sierra de los Tuxtlas.

Measurements of holotype.—Total length 110; length of tail 31; length of hind foot 14; condylobasal length 19.8; palatal length 8.4; maxillary breadth 6.8; interorbital breadth 5.3; length of maxillary toothrow 7.4; cranial breadth 10.7; length of M2 1.6.

Comparisons.—From *C. m. obscura* and *C. m. mexicana*, *C. m. nelsoni* differs in having slightly darker pelage and significantly larger external and

cranial dimensions (Table 1). From *C. m. peregrina*, *C. m. nelsoni* differs in having less highly developed front feet and claws, and darker ventral coloration.

Remarks.—To my knowledge, no specimens of *C. m. nelsoni* have been obtained since the series collected by Nelson and Goldman in 1894. The subspecies apparently is isolated on the Sierra de los Tuxtlas in Veracruz, and presently may be prevented from intergradation with *C. m. mexicana* by as much as 75 miles of tropical scrub forests and savannas not suited ecologically for habitation by the species. Goldman (1951:282-283) described the area at the site of capture of the holotype and paratypes of *nelsoni* as being covered with "heavy layers of volcanic sand and ashes" that quickly absorbed all surface moisture. The vegetation was said to consist of "virgin forest, including many fine trees. Among these were Spanish cedars, wild figs, and others of large size."

A reasonable argument could be made for recognition of *nelsoni* as a distinct species because the holotype and paratypes are significantly distinct from specimens from nearby populations of *mexicana*, and there is no indication of intergradation. Even so, *nelsoni* is no more distinct morphologically from *mexicana* than the other subspecies of *C. mexicana* recognized herein. It is noteworthy in this respect that, although specimens of *nelsoni* presently in collections are about the same size as specimens of *C. m. peregrina*, external and cranial features of *nelsoni* are less divergent from the primitive *mexicana* morphotype than are those of *peregrina*, even though the latter may intergrade with *mexicana* at the present time. Nevertheless, *nelsoni* probably can be regarded as an "incipient species" that is diverging from *C. mexicana* but is not yet sufficiently distinct morphologically to warrant specific recognition.

Specimens examined.—11, all from VERACRUZ, as follows: Volcán San Martín, 4800 ft., 11 (2 BMNH, 1 MCZ, 8 USNM).

***Cryptotis mexicana obscura* (Merriam)**

Blarina obscura Merriam, N. Amer. Fauna, 10:23, 31 December 1895.

Cryptotis obscura, Miller, Bull. U.S. Nat. Mus., 79:26, 31 December 1912; Hall and Kelson, The mammals of North America, 1:61, 31 March 1959; Hall and Dalquest, Univ. Kansas Publ., Mus. Nat. Hist., 14:206, 20 May 1963.

Cryptotis mexicana, Findley, Univ. Kansas Publ., Mus. Nat. Hist., 5:637, 1 December 1953; Koopman and Martin, Jour. Mamm., 40:4, February 1959.

Cryptotis mexicana madrea Goodwin, Amer. Mus. Novit., 1670:1, 28 June 1954, holotype from Rancho del Cielo, 5 mi. NW Gómez Farías, 3500 ft., Tamaulipas; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959; Alvarez, Univ. Kansas Publ., Mus. Nat. Hist., 14:396, 20 May 1963.

Holotype.—Subadult female, skin (adult summer pelage) and skull, U.S.

National Museum no. 55634, obtained on 27 August 1893 by E. W. Nelson, original number 5377; type locality, Tulancingo, 8500 ft., Hidalgo.

Distribution.—Sierra Madre Oriental from southwestern Tamaulipas to northeastern Querétaro and northern Hidalgo; interdigitates with *C. m. mexicana* where the borders of Hidalgo, Puebla, and Veracruz come into close proximity at about 20°00'-20°30' north latitude, 98°00'-98°30' west longitude (Fig. 6 and below).

Measurements of holotype.—Total length 89; length of tail 24; length of hind foot 13; condylobasal length 17.5; palatal length 7.4; maxillary breadth 5.5; interorbital breadth 4.5; length of maxillary toothrow 6.4; cranial breadth 8.8; length of M2 1.3.

Comparisons.—From *C. m. mexicana*, *C. m. obscura* differs in having slightly more reddish pelage, more darkly pigmented teeth, and significantly smaller external and cranial dimensions (Table 1). From *C. m. nelsoni* and *C. m. peregrina*, *C. m. obscura* differs in being smaller in every respect (Table 1).

Remarks.—Specimens assigned to *C. m. obscura* exhibit few external or cranial features (one exception being darkly pigmented teeth) that can be considered specializations over the primitive morphotype of *C. m. mexicana*. Mensural differences between *obscura* and *mexicana*, however, are pronounced, thus the two subspecies are well-differentiated and easily distinguished (see account of *C. m. mexicana*). Two specimens (UMMZ 89757-58) from Honey, Puebla, indicate intergradation with *mexicana* in mensural characters, but clearly are referable to *obscura* on the basis of pelage coloration and dental pigmentation. The village of Honey is located at about 7000 feet on the east-facing slope of the Sierra Madre Oriental near the boundary of cloud forest with upper humid tropical (pine-oak) forest that generally occurs higher on those slopes and on west-facing slopes. All other localities from which specimens referred to *obscura* have been obtained in the geographic region where the ranges of *obscura* and *mexicana* interdigitate are on relatively high west-facing slopes; all specimens referred to *mexicana*, on the other hand, are from cloud forests on east-facing slopes. It seems likely that additional collecting will reveal a narrow zone of intergradation where the vegetative zones meet, and that interdigititation of the ranges of the two subspecies will be shown to be considerably more complex than indicated by specimens presently available in museum collections.

Farther to the north, in the Gómez Farías region of Tamaulipas, the spatial relationship of cloud forest to upper humid tropical forest is maintained (Martin, 1958). The few specimens available for study from that region are larger, although not significantly so, than specimens of *obscura* from Hidalgo and Puebla, and it is noteworthy in

this respect that specimens from near Gómez Farías were collected in cloud forest rather than upper humid tropical forest. Although separated by a distance of more than 100 miles from the nearest locality to the south from which specimens identified as *obscura* have been examined, I consider the morphological differences between those populations insufficient to warrant formal recognition of the northern population, which was given the name *Cryptotis mexicana madrea* by Goodwin (1954a:1).

External and cranial dimensions exhibit clinal geographic variation among populations of *obscura*, becoming larger the farther from the zone of intergradation with *C. m. mexicana*. Thus, as with *C. m. mexicana*, an inverse subcline (representing geographic variation among populations of *C. m. obscura*) exists within the overall step-cline (representing geographic variation among subspecies of *C. mexicana*); specimens of *obscura* from the northern end of the range of the subspecies (near Gómez Farías, Tamaulipas) approach typical *mexicana* in mensural characteristics, whereas the two subspecies differ conspicuously in size near the zone of intergradation.

Cryptotis mexicana is known from subfossils from the Gómez Farías region of Tamaulipas (Koopman and Martin, 1959:4), and from late Pleistocene fossils from San Josecito Cave, near Aramberri, Nuevo León (Findley, 1953:637). Both records tentatively are referred to the subspecies *obscura* on geographic grounds.

Specimens examined.—48, as follows: TAMAULIPAS: Rancho del Cielo, 5 mi. NW Gómez Farías, 3500 ft., 5 (2 AMNH, *1 AMNH, 2 UMMZ); Aserradero del Infernillo, cave 11 mi. W Gómez Farías, 4400 ft., *10 (AMNH). VERACRUZ: Zacualpan, 6000 ft., 1 (KU). QUERÉTARO: Pinal de Amoles, 5500-9500 ft., 10 (2 UMMZ, 8 USNM). HIDALGO: Encarnación, 8200-9500 ft., 8 (USNM); Molango, ca. 5400 ft., 1 (UMMZ); Zacultipan, 3700-4500 ft., 8 (UMMZ); Lago Tejocotal, 11 km. E Acaxochitlán, ca. 7400 ft., 1 (KU); Tulancingo, 8500 ft., 2 (USNM). PUEBLA: Honey, ca. 7000 ft., 2 (UMMZ).

Cryptotis mexicana peregrina (Merriam)

Blarina mexicana peregrina Merriam, N. Amer. Fauna, 10:24, 31 December 1895.

C[ryptotis]. *mexicana peregrina*, Miller, Proc. Biol. Soc. Washington, 24:222, 31 October 1911.

Cryptotis mexicana peregrina, Hall and Kelson, The mammals of North America, 1:60, 31 March 1959; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:40, 30 April 1969 (part); Choate, Proc. Biol. Soc. Washington, 82:in press.

Cryptotis mexicana machetes, Musser, Oecas. Papers Mus. Zool., Univ. Michigan, 636:6, 17 June 1964; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:40, 30 April 1969 (part).

Notiosorex (Xenosorex) phillipsii Schaldach, Säugetierk. Mitt., 14:289, October 1966, holotype from Río Molino, 3 km. SW San Miguel Suchixtepec, 2250 m., Oaxaca; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:43, 30 April 1969 (part).

Holotype.—Subadult male, skin (adult summer pelage) and skull, U.S. National Museum no. 68317, obtained on 12 September 1894 by E. W. Nelson and E. A. Goldman, original number 6748; type locality, mountains 15 mi. SW Oaxaca de Juárez, 9500 ft., Oaxaca.

Distribution.—Sierra Madre del Sur in Oaxaca (Fig. 6).

Measurements of holotype.—Total length 106; length of tail 31; length of hind foot 15; condylobasal length 20.1; palatal length 8.8; maxillary breadth 6.5; interorbital breadth 5.1; length of maxillary toothrow 7.3; length of M2 1.5.

Comparisons.—From *C. m. obscura* and *C. m. mexicana*, *C. m. peregrina* differs in having significantly larger external and cranial dimensions (Table 1). From *C. m. nelsoni*, *C. m. peregrina* differs in having more highly developed front feet and claws, and paler ventral coloration. From *C. goldmani goldmani*, *C. m. peregrina* differs most noticeably in having much less highly developed front feet and claws, and darker (less olive or reddish) pelage.

Remarks.—The name *peregrina* is here applied to populations of *C. mexicana* that have become established on the Sierra Madre del Sur in Oaxaca, and have undergone morphological adaptations paralleling those of *C. goldmani* with which *peregrina* is sympatric. Specimens of *peregrina* can be distinguished readily from specimens of *goldmani* whenever the two species occur together in the same general area, but identification is more difficult where only one of the two species occurs. As discussed elsewhere, however, examination of front feet and claws or of a combination of external, cranial, and dental characters permits identification of every specimen. An interpretation of the zoogeographical significance of the relationship of *C. mexicana peregrina* to *C. goldmani goldmani* is presented in another section of this paper.

No specimens presently available show clear indications of intergradation between *C. m. peregrina* and *C. m. mexicana*, although a few specimens in the series of *mexicana* from Cerro San Felipe, Oaxaca, are as large as typical specimens of *peregrina*. The absence of obvious intergradation probably is due to insufficient sampling, inasmuch as the area in which intergradation might occur has been poorly collected. The hypothetical ranges of the two subspecies lie on either side of the Valley of Oaxaca; *peregrina* is known from 15 miles to the southwest of the valley at the type locality and *mexicana* is known from about nine miles to the north at Cerro San Felipe. Intergradation across the Valley of Oaxaca at the present time is unlikely, but intergradation may occur, and probably did in the past, across highlands to the north. The potential zone of intergradation is narrow, bordered to the north by lowlands associated with the Río Las Vueltas, Río Tomellín, and Río Grande. Thus, gene flow probably is highly restricted geographically if, indeed, any presently

occurs at all. Like *C. m. nelsoni*, *C. m. peregrina* might be considered an "incipient species"; however, it exhibits cranial and dental trends evident in other populations of *mexicana*, and therefore is regarded as a well-differentiated subspecies in the absence of evidence to the contrary.

Specimens of *peregrina* from the "coastal range" (south of the Río Atoyac and the Río Totolapan) in southern Oaxaca exhibit a pronounced tendency toward reduction of the dental formula. In every specimen the upper fourth unicuspids are greatly reduced and peg-like, and in many specimens one or the other, or both, of those teeth is missing altogether. Schaldach (1966:289) mistakenly assumed that specimens lacking both fourth upper unicuspids pertained to the genus *Notiosorex*, in which three unicuspids is the usual complement. Therefore, he described and named *Notiosorex phillipsii*, placing it in a separate subgenus (*Xenosorex*) characterized by its resemblance to *Cryptotis* in characters other than the dental formula. As demonstrated by Choate (1969), however, absence of the diminutive last upper unicuspids cannot be relied upon as an absolute generic character in blarinine shrews, as both *Cryptotis* and *Blarina* seemingly are undergoing reduction of the dental formula in certain populations at the present time (see also Choate, 1968). The three specimens (one lacking skull) on which Schaldach (*loc. cit.*) based the description of *Notiosorex (Xenosorex) phillipsii* are here referred to *Cryptotis mexicana peregrina*, although the specimen (UNAM 8447) lacking a skull conceivably may represent *C. goldmani goldmani*, as does the specimen reported (Schaldach, *op. cit.*:288) as *Cryptotis mexicana machetes* from the same locality.

Specimens examined.—47, as follows: OAXACA: La Muralla, Cerro Yucumino, 8 mi. S Tlaxiaco, ca. 10,500 ft., 1 (AMNH); 15 mi. SW Oaxaca de Juárez, 9500 ft., 24 (1 BMNH, 23 USNM); 20 mi. S, 5 mi. E Sola de Vega, 4800 ft., 1 (KU); Finca Sinai, 10 km. E Santos Reyes Nopala, 7200 ft., 2 (CAS); San Miguel Suchixtepec, 7300 ft., 10 (9 AMNH, 1 UMMZ); Río Molino, 3 km. SW San Miguel Suchixtepec, ca. 6800 ft., 2 (UNAM); Río Guajalote, S of San Miguel Suchixtepec, ca. 6000 ft., 1 (KU); 16 km. SW San Miguel Suchixtepec, ca. 6000 ft., 2 (ENCB); Río Jalatengo, S of San Miguel Suchixtepec, 4275 ft., 3 (CAS); Lovene, ca. 6000 ft., 1 (AMNH).

Cryptotis goldmani

(*Synonymy under subspecies*)

Distribution.—Cordillera Volcánica from at least as far east as Volcán Popocatépetl, Estado de México, westward to the Sierra de Autlán, Jalisco, thence southeastward in Guerrero and Oaxaca on the Sierra Madre del Sur and the Sistema Montañoso, thence eastward onto the Mesa Central in Chiapas, and finally southeastward onto the highlands of west-central Guatemala (Fig. 9).

Diagnosis.—External characteristics: size medium for the genus (Table 1);



FIG. 9. Geographic distribution of *Cryptotis goldmani alticola* (solid circles) and *C. goldmani goldmani* (open circles).

tail relatively short, averaging 34-40 per cent of length of head and body; front feet exceptionally large, with characteristically long, broad, and well-reinforced claws; all pelages distinctive; winter pelage luxuriant, with numerous vermiculations and a distinctive olive sheen, dorsum varying from Olive-Brown to Bister and venter considerably paler owing to pale buffy or whitish tips on the hairs; summer pelage with dorsum varying from Clove Brown to Mummy Brown (slight olivaceous sheen), and venter buffy, more grayish than in winter pelage because of added visual effect of gray bases of relatively short hairs; juvenile pelage "salt-and-pepper" gray dorsally in recently taken specimens (1967), nearer Clove Brown in older specimens (1894), consisting primarily of gray hairs tipped with Fuscous.

Cranial characteristics: rostrum relatively long; braincase angular; anterior limit of zygomatic plate above metastyle or between mesostyle and metastyle of M1; posterior limit of zygomatic plate at level of, or posterior to, maxillary process, above M3 or metastyle of M2; dentition not bulbous; anterior element of ectoloph of M1 slightly reduced relative to posterior element; posterior surfaces of P4-M2 decidedly recessed throughout most of geographic range (less so in Oaxaca); protoconal basin of M1 reduced relative to hypoconal basin; M3 usually consisting only of paracrista and precentrocrista (precentrocrista frequently vestigial in *C. g. alticola*), although postcentrocrista and rudimentary metacone sometimes present; talonid of m3 consisting only of hypoconid in *C. g. alticola*, but vestigial entoconid frequently present in *C. g. goldmani*.

Comparisons.—Comparisons with *C. goodwini*, *C. magna*, and *C. endersi* are given in the accounts of those species.

From *C. mexicana*, *C. goldmani* differs as follows: front feet and claws

substantially larger, usually flesh-colored as opposed to blackish; dorsal pelage olivaceous or reddish brown rather than blackish brown; ventral pelage paler, buffy or almost white in some specimens, as opposed to grayish brown or almost black; external and cranial dimensions generally averaging larger (Table 1); interorbital region usually narrowest posterior to proximal end of palate (level with proximal end of palate in *mexicana*); anterior element of ectoloph of M1 usually reduced relative to posterior element; posterior surfaces of P4-M2 usually more recessed; protoconal basin of M1 usually reduced relative to hypoconal basin; cingulae of molariform teeth scarcely elevated above gingivum (well elevated in *mexicana*); M3 more highly reduced, vestigial metaerista and hypocone almost never present; talonid of m3 almost never bearing fully-developed entoconid.

From *C. parva*, *C. goldmani* differs as follows: size uniformly and markedly larger (Table 1); front feet and claws substantially larger; braincase much more angular; talonid of m3 often having vestigial entoconid present in addition to well-developed hypoconid (entoconid never present in *parva*).

From *C. gracilis*, *C. goldmani* differs as follows: tail relatively and actually shorter, averaging 34-40 as opposed to 52 per cent of length of head and body; front feet and claws markedly larger; braincase more angular; posterior surfaces of P4-M2 usually considerably recessed, as opposed to slightly or not at all recessed; metacone on M3 much less highly developed.

Remarks.—The large relative size of the front feet and claws in *C. goldmani* is the most consistently diagnostic character by which the species can be distinguished from *C. mexicana*, and is especially useful in Oaxaca where the two species are sympatric and many otherwise diagnostic features converge, apparently as a result of parallel adaptations to shared environmental conditions. *Cryptotis goodwini* also has enlarged front feet and claws, but differs from *goldmani* in external size (total lengths in potentially sympatric populations 103-128 in *goodwini*, 101-111 in *goldmani*) and coloration (*goodwini* being the darker). Despite the array of names in synonymy, *goldmani* is not an extraordinarily variable species. Only two subspecies are recognized; all other proposed names have been applied to seasonal or age variants, and are here relegated to synonymy under one or the other of the two valid races.

Cryptotis goldmani is less generalized morphologically than *C. mexicana*, but is not so specialized dentally as *C. goodwini*. Within the known range of the species, morphological specialization is least pronounced in Oaxaca in the region of geographic sympatry with *mexicana*, and has reached progressively higher levels farther from that area.

The distribution of *goldmani* is restricted primarily to humid montane forests in western and southern México and western Guatemala. Elevations at which representatives of the species have been obtained vary as follows: 8200-10,500 feet on the Cordillera Vol-

cánica in the Distrito Federal; 8800-13,500 feet in Estado de México; 9000-12,000 feet in Michoacán; 8000-10,000 feet in Jalisco; 7500-10,300 feet on the Sierra Madre del Sur in Guerrero; 7000-10,500 feet on the Sierra Madre del Sur and Sistema Montañoso in Oaxaca; 500 feet on the Tehuantepec Plain of Oaxaca; 9500 feet on the Mesa Central of Chiapas; and 10,000 feet on the highlands of western Guatemala. The majority of specimens have been obtained in forests of fir (including Douglas-fir), pine, oak, and alder, frequently interspersed with large clumps of sacatón grass. In terms of biotic assemblages, *goldmani* resides primarily in the Canadian Zone of Goldman (1951:397-401), with some overlap into the Humid Upper Tropical Subzone. On the Tehuantepec Plain, however, the species occurs in xerophytic forest at elevations as low as 500 feet.

Available data on time of reproduction by *goldmani* are not so conclusive as for *mexicana*, but suggest that reproduction may occur throughout at least one-half of the year when all populations are considered together. Young individuals in juvenal pelage have been taken in June, July, September, and December; subadults have been collected in all months except January and August. As with *mexicana*, the portions of the year spent, respectively, in summer and winter pelage seemingly vary latitudinally and altitudinally, as do the times of molting. Individuals in summer pelage have been collected in the months of June through September; those molting from juvenal to summer pelage in June; those in winter pelage in October through May; and those molting from juvenal to winter pelage in September through December. One specimen that was molting from winter to summer pelage in March possibly represents an aberrant old adult.

Geographic variation.—On the basis of specimens presently available, *Cryptotis goldmani* does not exhibit substantial geographic variation. The population (sample 3) that inhabits the Sierra Madre del Sur in Guerrero has the smallest means for total length, length of hind foot, and length of maxillary toothrow. Populations to the north (sample 1) and northwest (sample 2) of Guerrero on the Cordillera Volcánica have means toward the upper limit of variation in most measurements, especially length of maxillary toothrow and length of M2, in which specimens from those populations are significantly larger than those from all other populations sampled. Specimens from populations (samples 4, 5, and 6) to the east and southeast of Guerrero usually are larger, although seldom significantly so, than specimens from the latter state.

The only notable trend in geographic variation in *C. goldmani*,

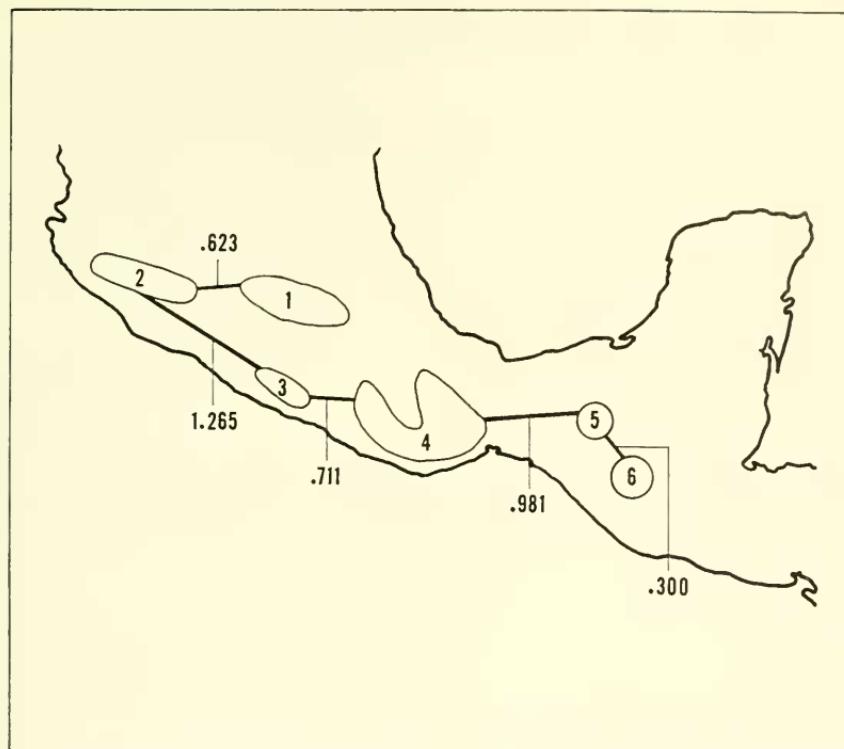


FIG. 10. Semi-diagrammatic representation of geographic relationships of samples of *Cryptotis goldmani*. Localities included in numbered samples are listed in Methods and Materials. Distance coefficients are illustrated for all potential routes of gene flow; the lower the coefficient, the greater the resemblance (see text).

therefore, involves slightly smaller average size in the population in Guerrero than in populations on either side of Guerrero. The differences between the means of most measurements are greater between the population at the western end of the Cordillera Volcánica, in the vicinity of Nevado de Colima, Jalisco (sample 2), and that in Guerrero (sample 3) than between the latter and the adjacent population (sample 4) in Oaxaca. As a result, the distance coefficient (Fig. 10) calculated from all mensural characters is greater between samples 2 and 3 (1.265) than that between samples 3 and 4 (.711). The high distance coefficient between samples 2 and 3 corresponds geographically to the Balsas Basin, and probably can be interpreted to imply actual lack of gene flow across habitat not presently suited for habitation by the species. Likewise, a relatively high distance coefficient (.981) exists between samples 4 and 5, corresponding geographically to populations on either side of the Isthmus of Tehuantepec.

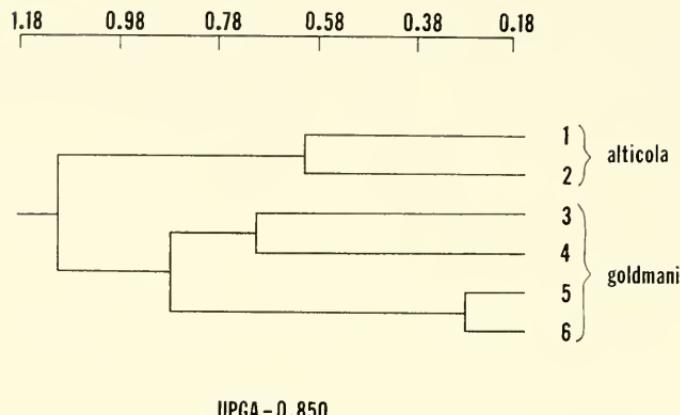


FIG. 11. Phenogram of numbered samples (see Fig. 10) of *Cryptotis goldmani* computed from distance matrices on standardized characters and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram is 0.850. Subspecific assignment is indicated to the right of the sample number.

tepec; this would seem to indicate at least retarded gene flow (perhaps only recently so) across the isthmus that has resulted in slight divergence, but which is not considered to warrant subspecific recognition. Presentation of the results of phenetic analysis in the form of a phenogram (Fig. 11) computed from distance matrices further demonstrates the apparent break in gene flow across the Balsas Basin (between samples 2 and 3) and the lesser break across the Isthmus of Tehuantepec (between samples 4 and 5).

Geographic variation of qualitative characters provides additional justification for recognition of only two subspecies of *C. goldmani*—one (*alticola*) on the Cordillera Volcánica in the Distrito Federal, the Estado de México, Michoacán, and Jalisco (samples 1 and 2), and the other (*goldmani*) on the Sierra Madre del Sur in Guerrero and Oaxaca, the Sistema Montañoso in Oaxaca, and across the Isthmus of Tehuantepec onto the Mesa Central of Chiapas and the highlands of western Guatemala (samples 3, 4, 5, and 6). Specimens from populations on the Cordillera Volcánica have undergone complete reduction of the entoconid of m3, generally have a reduced metacone on M3, and have deeply emarginate posterior surfaces on the upper molariform teeth; specimens of the nominate subspecies, on the other hand, retain more nearly primitive dental configurations, and demonstrate no obvious breaks in clinal geographic variation of cranial or dental features across the Isthmus of Tehuantepec.

Cryptotis goldmani alticola (Merriam)

Blarina alticola Merriam, N. Amer. Fauna, 10:27, 31 December 1895.

Cryptotis alticola, Miller, Bull. U.S. Nat. Mus., 79:27, 31 December 1912; Davis, Jour. Mamm., 25:376, 12 December 1944; Hooper, Occas. Papers Mus. Zool., Univ. Michigan, 586:3, 30 April 1957; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959; Genoways and Choate, Proc. Biol. Soc. Washington, 80:204, 1 December 1967.

Cryptotis euryrhynchis Genoways and Choate, Proc. Biol. Soc. Washington, 80:203, 1 December 1967, holotype from Volcán de Fuego [also called Volcán de Colima], 9800 ft., Jalisco.

Holotype.—Subadult male, skin (adult winter pelage) and skull, U.S. National Museum no. 52047, obtained on 25 February 1893 by E. W. Nelson, original number 4396; type locality, Volcán Popocatépetl, 11,500 ft., Estado de México.

Distribution.—Cordillera Volcánica from Volcán Popocatépetl, Estado de México, in the east to the Sierra de Aulán, Jalisco, in the west (Fig. 9); probably also occurs in Nayarit and Colima, and on the Sierra de Coalcomán in Michoacán.

Measurements of holotype.—Total length 107; length of tail 26; length of hind foot 15; condylobasal length 20.5; palatal length 9.0; maxillary breadth 6.8; interorbital breadth 5.2; length of maxillary toothrow 7.3; cranial breadth 10.3; length of M2 1.6.

Comparisons.—From *C. g. goldmani*, *C. g. alticola* differs in having significantly larger external and cranial dimensions (Table 1) and more highly reduced and specialized dentition.

Remarks.—*Cryptotis goldmani alticola* is the more highly specialized of the two subspecies of *C. goldmani* recognized. The most notable dental specialization is elimination of the entoconid on the talonid of m3. Entoconids are prevalent on that tooth in more than 50 per cent of specimens of *goldmani* examined from Oaxaca; occasionally they are fully-developed, but more frequently they are reduced. Vestigial entoconids occur in about 50 per cent of specimens of *goldmani* from Guerrero, although only a few are fully developed. I have seen no specimen of *alticola*, however, having even a vestigial entoconid. Paralleling reduction of the talonid of m3, there is progressively greater posterior emargination of the upper molariform teeth in *alticola*, and there are other cranial and dental specializations.

Genoways and Choate (1967:203) described and named as *Cryptotis euryrhynchis* the population of *C. goldmani* that inhabits Volcán de Fuego and Nevado de Colima, Jalisco. Criteria for distinguishing *euryrhynchis* from *alticola* were large size and dark color. With larger samples available for comparison of the two populations, it now is apparent that the slight difference in size be-

tween the two is not statistically significant (Table 1). Furthermore, specimens now available from geographically intermediate areas in Michoacán (near Ciudad Hidalgo and on Cerro Tancítaro) are almost intermediate in size between specimens from the eastern and western ends of the Cordillera Volcánica. Study of color of specimens collected subsequent to the description of *euryrhynchis* has demonstrated that the differences used to distinguish that population from *alticola* are due in part to foxing of the holotype and paratypes of *alticola* (when compared to the fresh pelage of the holotype of *euryrhynchis*).

Intergradation between *alticola* and the nominate subspecies is doubtful at present. The geographic ranges of the two subspecies are separated at the borders of Michoacán and Guerrero, where the Río Balsas demarcates the Sierra Madre del Sur from the Sierra de Coalcomán; the Balsas Basin is arid and the dominant vegetation is low, xerophilous, deciduous thorn scrub forest (see also Duellman, 1965:643). The break in gene flow between populations to the northwest and southeast of the Balsas Basin, although undoubtedly complete, apparently has not been in effect for a long enough time to permit sufficient morphological divergence to warrant recognition of *alticola* as a distinct species. As is the case for several other taxa recognized herein as subspecies, the term "incipient species" is appropriate in that continued isolation probably will effect speciation. No proof is available that individuals of *alticola* could interbreed with individuals of *goldmani* under natural conditions, but, in the absence of data from biosystematic analyses, "degree of difference" (Hall, 1943:142; Mayr *et al.*, 1953:103-104) was used as the criterion for classifying *alticola* as a subspecies of *C. goldmani* rather than as a distinct species of the *mexicana*-group. As in other mammalian groups that presently have "insular distributions" and are scattered through the Mexican highlands, *C. goldmani* is particularly in need of study by serological and cytological methods in order to assess better the evolutionary significance of breaks in gene flow between populations that occur in identical habitats at about the same latitude and elevation, and which therefore may not face substantial selective pressure to undergo morphological divergence.

Specimens examined.—33, as follows: JALISCO: 20 mi. SE Autlán, 9000 ft., 3 (KU); 12 mi. SW Ciudad Guzmán, 10,000 ft., 3 (KU); Volcán de Fuego, 9800 ft., 1 (KU); N slope Nevado de Colima, 8000-10,000 ft., 4 (2 ALG, 2 WGB). MICHOACÁN: 12 mi. W Ciudad Hidalgo, 9150 ft., 1 (KU); Cerro de Tancitaro, 9000-12,000 ft., 3 (USNM). ESTADO DE MÉXICO: Salazar, 8800-10,500 ft., 3 (USNM); Cerro Ajusco, 11,000 ft., 1 (USNM); Lagunas de Zempoala, 10 mi. NWN Cuernavaca, Morelos, 9100 ft., 3 (USNM); 12 km. ESE Amecameca, 11,500 ft., 1 (KU); N slope Nevado de Toluca, 11,500 ft., 1 (USNM); Volcán Popocatépetl, 11,500-13,500 ft., 5 (1 BMNH, 4 USNM).

DISTRITO FEDERAL: N edge Refugio San Cayetano, 3 mi. S Bosenchere, 8200 ft., 1 (UMMZ); Cerro de Santa Rosa, 10,000-10,500 ft., 2 (1 UMMZ, 1 UNAM); Cañon Contreras, 10,200 ft., 1 (UMMZ).

***Cryptotis goldmani* (Merriam)**

Blarina mexicana goldmani Merriam, N. Amer. Fauna, 10:25, 31 December 1895.

Blarina mexicana machetes Merriam, N. Amer. Fauna, 10:26, 31 December 1895, holotype from mountains near Santa María Ozolotepec, 10,000 ft., Oaxaca.

Blarina fossor Merriam, N. Amer. Fauna, 10:28, 31 December 1895, holotype from Cerro Zempoaltepec, 10,500 ft., Oaxaca.

Cryptotis frontalis Miller, Proc. Biol. Soc. Washington, 24:222, 31 October 1911, holotype from "near Tehuantepec City," Oaxaca; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:41, 30 April 1969.

Cryptotis mexicana goldmani, Miller, Bull. U.S. Nat. Mus., 79:27, 31 December 1912; Davis and Lukens, Jour. Mamm., 39:350, 20 August 1958; Hall and Kelson, The mammals of North America, 1:59, 31 March 1959; Genoways and Choate, Proc. Biol. Soc. Washington, 80:204, 1 December 1967.

Cryptotis mexicana machetes, Miller, Bull. U.S. Nat. Mus., 79:27, 31 December 1912; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959; Schaldach, Säugetierk. Mitt., 14:288, October 1966; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:40, 30 April 1969 (part).

Cryptotis fossor, Miller, Bull. U.S. Nat. Mus., 79:27, 31 December 1912; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:41, 30 April 1969.

Cryptotis guerrerensis Jackson, Proc. Biol. Soc. Washington, 46:80, 27 April 1933, holotype from Omilteme, about 8000 ft., Guerrero; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959.

Cryptotis griseoventris Jackson, Proc. Biol. Soc. Washington, 46:80, 27 April 1933, holotype from San Cristóbal de las Casas, 9500 ft., Chiapas; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959.

Notiosorex (Xenosorex) phillipsii, Goodwin, Bull. Amer. Mus. Nat. Hist., 141:43, 30 April 1969 (part).

Cryptotis mexicana mexicana, Jones and Genoways, Jour. Mamm., 48:321, 20 May 1967; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:39, 30 April 1969 (part).

Holotype.—Subadult male, skin (adult winter pelage) and skull, U.S. National Museum no. 70244, obtained on 23 December 1894 by E. W. Nelson and E. A. Goldman, original number 7231; type locality, mountains near Chilpancingo, 9600 ft., Guerrero.

Distribution.—Sierra Madre del Sur in Guerrero and southwestern Oaxaca and the Sistema Montañoso in northeastern Oaxaca, thence across the Isthmus of Tehuantepec to the Mesa Central of Chiapas and southeastward onto the highlands of Guatemala at least as far as Todos Santos (Fig. 9).

Measurements of holotype.—Total length 100; length of tail 28; length of hind foot 13; condylobasal length 19.5; palatal length 8.5; interorbital breadth 4.9; length of maxillary toothrow 7.0; cranial breadth 10.0; length of M2 1.5.

Comparisons.—From *C. g. alticola*, *C. g. goldmani* differs in having significantly smaller external and cranial dimensions (Table 1) and less reduced and specialized dentition.

Remarks.—As implied by the lengthy synonymy, more populations here included under the name *C. g. goldmani* have been named as distinct taxa than in any other representative of the genus *Cryptotis*. Some of the confusion, as alluded to earlier, resulted from failure to distinguish between *C. goldmani* and *C. mexicana*. Merriam (1895:27) clearly distinguished between *Blarina alticola* and typical *Blarina mexicana*, but failed to note similarities between *Blarina mexicana goldmani* and *Blarina mexicana machetes*. He (*op. cit.*:28) recognized the relationship between *Blarina fossor* and *Blarina alticola*, but failed to compare either with *Blarina mexicana machetes*. Miller (1911:222) compared *Cryptotis frontalis* with typical *mexicana*, but not with either *fossor* or *machetes*. Likewise, Jackson (1933:81) compared *Cryptotis griseoventris* with typical *mexicana*, but not with either *machetes* or *fossor*. Thus, the typological approach to the study of relationships was the primary source of the chaotic array of names that now appear in the synonymy of *C. g. goldmani*.

Davis and Lukens (1958:350) demonstrated conclusively that the characteristics by which Jackson (1933:80) distinguished *Cryptotis guerrerensis* from *Cryptotis mexicana goldmani* actually were the result of age and seasonal variation rather than genetic differences. Additional specimens now available from near the type locality of *guerrerensis* substantiate their contention that the two named kinds are synonymous. Similarly, the only real differences among populations that were given the names *fossor*, *machetes*, *griseoventris*, and *goldmani* are seasonal rather than genetic: the holotype and paratypes of *fossor* are in a mixture of short summer pelage and even shorter juvenal pelage; the type series of *machetes* is in luxuriant winter pelage; the type series of *goldmani* is in worn winter pelage; the type series of *griseoventris* includes a mixture of specimens in juvenal pelage, specimens undergoing post-juvenal molt, and specimens in adult summer pelage. There are no consistently diagnostic qualitative features by which any of the populations on which these names were based can be recognized, and none differs significantly in mensural characteristics.

It is noteworthy that specimens from the Mesa Central of Chiapas and the highlands of western Guatemala do not differ significantly from specimens from populations west of the Isthmus of Tehuantepec, even though damp fir forests of the kind usually

frequented by *goldmani* are scarce, at least at present, on the isthmus (see also Duellman, 1960:32). However, specimens from the District of Tehuantepec in Oaxaca have been collected in relatively xeric pine forest, perhaps indicating that gene flow is continuous, although retarded, across the isthmus at the present time.

Specimens examined.—74, as follows: CUERRERO: 3 mi. NW Omilteme, ca. 7500 ft., 1 (USNM); 3 mi. W Omilteme, 8200 ft., 1 (MVZ); 2 mi. W Omilteme, 7800-7900 ft., 4 (TCWC); Omilteme, 7300-8000 ft., 9 (3 KU, 6 USNM); mountains NW Chilpancingo, 9600-9800 ft., 5 (1 BMNH, 4 USNM); S slope Cerro Teotepec, ca. 10,300 ft., 1 (UMMZ). OAXACA: 6½ mi. SSW Vista Hermosa, 7100 ft., 1 (KU); 11 mi. NE Llano de las Flores, 9100 ft., 1 (UMMZ); 2 km. NE San Andres Chicahuaxtla, ca. 7500 ft., 1 (UMMZ); Cerro Zempoaltepec, 8000-10,500 ft., 5 (1 BMNH, 4 USNM); Mixteguilla, ca. 500 ft., 2 (AMNH); "near the City of Tehuantepec," ca. 500 ft., 1 (USNM); Lachao, ca. 7000 ft., 1 (AMNH); mountains near Santa María Ozolotepec, 10,000 ft., 8 (1 BMNH, 7 USNM); San Juan Ozolotepec, ca. 7500 ft., 1 (AMNH); San Miguel Suchixtepec, ca. 9000 ft., 2 (AMNH); 3 km. SW San Miguel Suchixtepec, ca. 7400 ft., 1 (UNAM). CHIAPAS: San Cristóbal de las Casas, 9500 ft., 9 (USNM); 6 mi. SE San Cristóbal de las Casas, ca. 7000 ft., 1 (MCZ). GUATEMALA: Todos Santos Cuchumatán, 10,000 ft., 19 (USNM).

Cryptotis goodwini Jackson

Cryptotis goodwini Jackson, Proc. Biol. Soc. Washington, 46:81, 27 April 1933; Goodwin, Bull. Amer. Mus. Nat. Hist., 68:6, 12 December 1934; Felten, Senckenbergiana Biologica, 39:218, 15 December 1958; Hall and Kelson, The mammals of North America, 1:61, 31 March 1959; Genoways and Choate, Proc. Biol. Soc. Washington, 80:204, 1 December 1967.

Cryptotis nigrescens, Burt and Shirton, Misc. Publ. Mus. Zool., Univ. Michigan, 117:21, 22 September 1961 (part).

Cryptotis. *goodwini*, Musser, Occas. Papers Mus. Zool., Univ. Michigan, 636:7, 17 June 1964.

Holotype.—Adult male, skin (adult winter pelage) and skull, U.S. National Museum no. 77074, obtained on 13 January 1896 by E. W. Nelson and E. A. Goldman, original number 9073; type locality, Calel, 10,200 ft., Quezaltenango, Guatemala.

Distribution.—Highlands of southern Guatemala and western El Salvador (Fig. 6); possibly also on the Sierra Madre of Chiapas and the highlands of western Honduras.

Measurements of holotype.—Total length 117; length of tail 28; length of hind foot 15.5; condylobasal length 21.1; palatal length 9.3; maxillary breadth 7.2; interorbital breadth 5.9; length of maxillary toothrow 7.9; cranial breadth 11.1; length of M2 1.7.

Diagnosis.—External characteristics: size large for the genus (Table 1); tail short, averaging 35 per cent of length of head and body; front feet and claws large; juvenal pelage unknown; adult summer and winter pelages distinctive; winter pelage luxuriant with numerous vermiculations, dorsum near Bister in old specimens (1896), but nearer Clove Brown in recently taken specimens (1954-1955), venter paler because of admixture of pale buff- or white-tipped hairs; summer pelage not especially luxuriant, a few vermiculations sometimes

present when pelage is fresh, dorsum Bister in specimens obtained in 1926, Clove Brown in specimens obtained in 1947, venter only slightly paler.

Cranial characteristics: rostrum relatively long, slender; braincase not especially angular; anterior limit of zygomatic plate above metastyle of M1; posterior limit of zygomatic plate at level of or posterior to maxillary process, above M3; dentition not bulbous; anterior element of ectoloph of M1 reduced relative to posterior element; posterior surfaces of P4-M2 decidedly recessed; protoconal basin of M1 reduced relative to hypoconal basin; M3 consisting primarily of paracrista, precentrocrista usually vestigial and frequently absent; talonid of m3 reduced, short, consisting only of hypoconid, which frequently is vestigial.

Comparisons.—Comparisons with *C. mexicana*, *C. magna*, and *C. nigrescens* are given in the accounts of those species.

From *C. goldmani*, *C. goodwini* differs as follows: size larger, both externally and cranially (Table 1); pelage slightly darker; braincase less angular; M3 more reduced, precentrocrista seldom present and metacone never present (either or both sometimes present in *goldmani*); talonid of m3 more reduced, consisting only of hypoconid, which frequently is vestigial.

From *C. gracilis*, *C. goodwini* differs as follows: size notably larger, both externally and cranially (Table 1); tail relatively and actually much shorter, averaging 35 (as opposed to 52) per cent of length of head and body; front feet and claws markedly larger; posterior surfaces of P4-M2 considerably more recessed; M3 much more reduced, metacone and postcentrocrista never present (always present in *gracilis*); talonid of m3 reduced, entoconid never present.

From *C. endersi*, *C. goodwini* differs as follows: size notably larger, both externally and cranially (Table 1); tail relatively and actually much shorter, averaging 35 (as opposed to 49) per cent of length of head and body; front feet and claws markedly larger; rostrum relatively shorter; dentition not bulbous; anterior element of ectoloph of M1 reduced relative to posterior element; posterior surfaces of P4-M2 recessed; protoconal basin of M1 reduced relative to hypoconal basin; M3 much more reduced, metacone absent; talonid of m3 more reduced, entoconid never present (entoconid present but vestigial in *endersi*).

Remarks.—*Cryptotis goodwini* is the most highly specialized member of the *mexicana*-group. In addition to possessing well-developed front feet and claws characteristic of *C. goldmani*, the species *goodwini* exhibits more extreme reduction of dentition than any other Middle American representative of the genus. The talonid of m3 in *goodwini* never consists of more than one cusp, and that cusp (the hypoconid) is vestigial in many specimens. The third upper molar generally has become reduced to a single bladelike crista (the paracrista). Emargination of the upper molariform teeth is more pronounced than in either *mexicana* or *goldmani*, and approaches the most extreme situation found in Mexican populations of *C. parva*.

The known distribution of *C. goodwini* is restricted primarily to humid montane forests in the southern half of Guatemala and adjacent El Salvador. Elevations on major topographic features from which representatives of the species have been obtained vary

as follows: 9500-11,000 feet on the Alto Cuchumatanes; approximately 3000 feet on the Sierra de Xucaneb; 6000-10,000 feet on the Sierra de Chuacús; and approximately 4000-11,000 feet on the Sierra Madre de Guatemala. The majority of specimens have been obtained in forests of pine or oak, frequently mixed with cypress, fir, or alder, and often including abundant sacatón or mosses. These elevations and habitats could be construed to pertain to the Canadian and Humid Upper Tropical life zones of Goldman (1951), and are included in the subtropical life belt of Stewart (1950) and the subtropical and temperate life belts of Griscom (1932). *Cryptotis goodwini* is too poorly known ecologically to warrant more than a general account of its distribution, but it is noteworthy that the species exhibits no apparent geographic variation throughout its known range on the various highland masses of Guatemala.

Felten's (1958:218) report of a specimen of *goodwini* from Hacienda Montecristo, El Salvador, constitutes the only record for the species from that country. Without examining the specimen, Burt and Stirton (1961:21) listed the record under *C. nigrescens*, probably because they had examined specimens of *nigrescens* from localities near that from which Felten's specimen was obtained. Cranial measurements listed in Felten's report (condylobasal length 20.7; cranial breadth 10.9), however, are much too large for *nigrescens* and agree well with measurements of *goodwini*.

Each of a series of seven adult males (UMMZ 112004-10) caught on Cumbre María Tucum on 20 August 1962 had enlarged testes. The weights of those males ranged from 15.7 to 18.7 grams; an adult female (UMMZ 112011) caught at that locality on the same date weighed 16.2 grams.

Specimens examined.—37, all from GUATEMALA, as follows: 3½ mi. SW San Juan Ixcoy, 10,120 ft., 1 (KU); *Hacienda Chancol*, 15 mi. W Nebaj, 9500-11,000 ft., 1 (USNM); Finca Xicacao, ca. 3000 ft., 1 (UMMZ); S slope Volcán Tajamulco, 10,000 ft., 1 (UMMZ); Finca La Paz, ca. 4000 ft., 2 (UMMZ); Calel, 10,200 ft., 14 (USNM); Cumbre María Tucum, ca. 9900 ft., 8 (UMMZ); Santa Elena, 9900-10,000 ft., 4 (FMNH); Tecpán, 9700 ft., 1 (AMNH); Volcán Santa María, 9000-11,000 ft., 2 (USNM); 5 mi. N, 1 mi. W Santa Cruz El Chol, 6000 ft., 1 (KU); Mataquesuintla, 8400 ft., 1 (USNM).

Additional record.—EL SALVADOR: Hacienda Montecristo, Santa Ana (Felten, 1958:218).

Cryptotis parva-group

Cryptotis parva

(*Synonymy* under subspecies)

Distribution.—Southward from the eastern United States in mesic areas of northeastern México from at least as far west as Ciudad Acuña and Melchor Múzquiz on the Río Grande and its tributaries in Coahuila, across northern

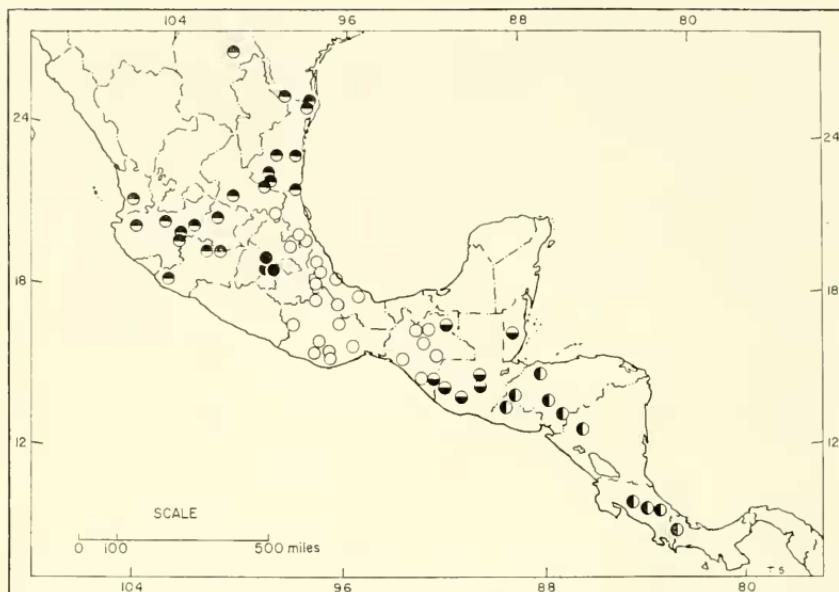


FIG. 12. Geographic distribution of *Cryptotis parva*. Circles half solid above, *C. parva berlandieri*; solid circles, *C. parva soricina*; open circles, *C. parva pueblensis*; circles half solid below, *C. parva tropicalis*; circles half solid left, *C. parva orophila*.

Nuevo León and Tamaulipas to the Gulf coastal lowlands, southward in the lowlands and on the Sierra Madre Oriental in Tamaulipas and probably Nuevo León, thence southward and westward across the Mexican Plateau to the Valley of Mexico and the Cordillera Volcánica; on the Sierra Madre Oriental in Veracruz and Puebla, and on the Sistema Montañoso and the Sierra Madre del Sur in Oaxaca, thence across the Isthmus of Tehuantepec and onto the Mesa Central and the Sierra Madre in Chiapas, the Sierra Madre in Guatemala, and highlands of British Honduras, Honduras, El Salvador, and north-central Nicaragua; also on the cordilleras of Costa Rica and the Chiriquí region of Panamá (Fig. 12).

Diagnosis.—External characteristics: size small for the genus (Table 1); tail short, averaging 29-37 per cent of length of head and body; front feet and claws small; juvenal and adult summer pelages frequently not distinctive, overall appearance "salt-and-pepper" gray or grayish brown, juvenal pelage characteristically lacking basal gray region; adult winter pelage always distinctive, relatively luxuriant, with vermiculations numerous only at higher elevations (vermiculations usually faint or lacking elsewhere), overall appearance "salt-and-pepper" brown or dark brown (precise color determinations given in accounts of subspecies).

Cranial characteristics: rostrum short; braincase not especially angular, almost pentagonal in shape; anterior limit of zygomatic plate varying from slightly anterior to mesostyle of M1 to above metastyle of that tooth; posterior limit of zygomatic plate above, or slightly anterior to, maxillary process; dentition not bulbous; anterior element of ectoloph of M1 reduced relative to posterior element; posterior surfaces of P4-M2 decidedly recessed (less so in southern

México and Guatemala); protoconal basin of M1 reduced relative to hypoconal basin; M3 usually consisting only of paracrista and precentrocrista, the latter sometimes reduced or absent (vestigial postcentrocrista or metacone present in a few specimens); talonid of m3 consisting only of hypoconid.

Comparisons.—Comparisons with *C. mexicana*, *C. goldmani*, *C. endersi*, and *C. gracilis* are given in the accounts of those species.

From *C. nigrescens*, *C. parva* differs as follows: pelage usually paler, especially ventrally; size generally smaller (Table 1); dentition not bulbous; anterior element of ectoloph of M1 reduced relative to posterior element; posterior surfaces of P4-M2 considerably recessed (not at all recessed in *nigrescens*); protoconal basin of M1 reduced relative to hypoconal basin.

From *C. goodwini*, *C. parva* differs as follows: size conspicuously smaller, both externally and cranially (Table 1); rostrum relatively and actually shorter; M3 less reduced, metacone and precentrocrista sometimes present (never present in *goodwini*).

From *C. magna*, *C. parva* differs as follows: size conspicuously smaller, both externally and cranially (Table 1); tail relatively and actually shorter, averaging 29-37 (as opposed to 52) per cent of length of head and body; pelage usually paler, especially ventrally; dentition not bulbous (moderately bulbous in *magna*); posterior surfaces of P4-M2 considerably recessed; protoconal basin of M1 reduced relative to hypoconal basin; M3 considerably more reduced; talonid of m3 consisting only of hypoconid (both hypoconid and well-developed entoconid always present in *magna*).

Remarks.—*Cryptotis parva* can be distinguished under field conditions from all other species in the genus except *C. nigrescens* solely on the basis of its small external size. Adults of *parva* can be segregated readily by their pale (almost white) ventral coloration from specimens of *nigrescens* of any age. In labial view, the upper and lower unicuspids of *parva* appear relatively small, slender, and bladelike; in *nigrescens*, on the other hand, the unicuspids appear larger, rounded, and not at all bladelike.

Unlike that of most other representatives of the genus, the hair of *parva* retains more-or-less generalized agouti characteristics, which are most noticeable in winter pelage. It has been suggested by Hershkovitz (1968) that the agouti pattern is primitive in mammals, and that change from the agouti pattern is directional and predictable. This hypothesis is debatable (Lawlor, 1969); nevertheless it is of interest that *parva*, with its agouti-type pelage, shows more geographic variation in color than any other species in the genus. In contrast to the generalized pelage characteristics, the skull and dentition of *C. parva* are highly specialized. Features of the teeth, such as reduction of M3 and m3 and posterior emargination of P4-M2, are advanced beyond those of the other species (*C. nigrescens*) herein referred to the *parva*-group, and the antiquity of these features is attested to by the fossil record.

Five subspecies of *C. parva* are recognized here from Middle America. One of these subspecies, *C. p. berlandieri*, also occurs in the United States, and four additional nominal subspecies are known only from the United States and extreme southern Canada (Hall and Kelson, 1959:56-58). The status of the subspecies occurring north of México will be reviewed in a later paper.

The distribution of *C. parva* in Middle America is restricted primarily to mesic habitats near permanent sources of water. Elevations at which representatives of the species have been obtained vary as follows: 30-1050 feet along the Río Grande at the border between Texas and México; 1600 feet near a tributary of the Río Grande in Coahuila; from 30 feet on the Gulf coastal plain to 3400 feet on the Sierra Madre Oriental in Tamaulipas; 2000-7300 feet on the Mexican Plateau in San Luis Potosí and Guanajuato; 5000-6600 feet on the Cordillera Volcánica and associated highlands in Jalisco; 3100 feet on the northwesternmost slopes of the Cordillera Volcánica (more specifically, the Sierra de Autlán) in Nayarit; 4250-8000 feet on the Cordillera Volcánica and 8900 feet on the Sierra de Coalcomán in Michoacán; 4100-7600 feet in the Valley of Mexico in Estado de México and Distrito Federal; 400 feet on the western slope of the Sierra Madre Oriental in San Luis Potosí; from 30 feet on the Gulf coastal plain to 6500 feet on the Sierra Madre Oriental in Veracruz; from 800 feet on the Gulf coastal plain to 3300 feet on the Sierra Madre Oriental in Puebla; from 300 feet in the Caribbean lowlands to 4900 feet on the Sistema Montañoso and 2400-6600 feet on the Sierra Madre del Sur in Oaxaca; 3000-7800 feet on the Mesa Central and 500-4600 feet on the Sierra Madre in Chiapas; 3200-4900 feet on the Sierra Madre in Guatemala; 1000 feet on the highlands of British Honduras; 2500-5500 feet on the highlands of Honduras; 4000-5000 feet on the Cordillera Isabella in Nicaragua; 3800-7750 feet on the Cordillera Central, Cordillera de Talamanca, and intervening regions in Costa Rica; and 3600-6800 feet on the Cordillera de Talamanca in the Chiriquí region of Panamá.

Although *C. parva* is primarily a grassland species, its distribution apparently is not restricted by strict preference for any biotic association. Rather, the species occurs ubiquitously in habitats varying from mesic borders along permanent sources of water where the dominant vegetation away from the stream may consist of mesquite, yucca, or agave, to grass-covered llanos, scrubby live oak or pine-oak forests, dense humid tropical forests, or cloud forests. Using Goldman's (1951) arrangement of biotic associations, this diversity of habitat would include the Lower Austral, Upper Austral, Arid

Lower Tropical, Arid Upper Tropical, Humid Lower Tropical, and Humid Upper Tropical life zones. Judging from series of specimens presently in collections, the species is most easily caught in large numbers in restricted damp or mesic areas, such as at the borders of streams or lakes, within otherwise relatively arid habitats.

Available data on reproduction in Middle American populations of *C. parva* indicate that females probably bear young throughout the year, at least at certain elevations and latitudes, but that the peak of reproduction occurs between the vernal equinox and autumnal equinox. Individuals classified as young on the basis of dentition and pelage have been collected in every month except March and May. Likewise, subadults, adults, and old adults are evenly distributed throughout the seasons. Specimens in collections for which there are data on reproductive condition are few: an adult female (KU 54923) caught on 6 June 1953 at a place 2 mi. S and 10 mi. W Piedra, Tamaulipas, was lactating; an adult female (KU 54924) caught on 5 July 1953 at a place 1 mi. S Altamira, Tamaulipas, had three embryos that measured 5 mm. in crown-rump length; an adult male and female (AMNH 164871-72) from 6 mi. N Rancho del Tigre, Tamaulipas, were caught together in a nest with four young on 22 April 1953 (see also Goodwin, 1954c:3); an adult female (UMMZ 93144) that was caught on 26 May 1948 at a place 3 mi. E Pátzcuaro, Michoacán, contained six embryos that measured 3 mm. in crown-rump length; an old adult female (CAS 14311) from approximately 6 mi. N Puerto Escondido, Oaxaca, was lactating when caught on 10 August 1965.

Molt, like reproduction, apparently is influenced by elevation, latitude, and associated environmental factors. Individuals in adult summer pelage have been collected in March, April, June through August, and November; those molting from summer to winter pelage in December; those in winter pelage from November through July; those molting from juvenal to winter pelage in September, November, and December; those molting from winter to summer pelage in March and June. The amount of overlap between winter and summer pelage, which is greater in *parva* than in other species of *Cryptotis*, may be attributed to the variable range, in both latitude and altitude, of this species.

Geographic variation.—The general trend in geographic variation of external and cranial dimensions among Middle American populations of *Cryptotis parva*, with few exceptions, is for size to increase with decreasing latitude as far south as Guatemala, and then to decrease irregularly southward from Guatemala.

Geographic variation in total length is relatively typical of the general pattern for external measurements. Populations along the Río Grande and its tributaries in southernmost Texas and north-eastern México (sample 1), in mesic regions associated with, or on either side of, the Sierra Madre Oriental in Tamaulipas and San Luis Potosí (sample 2), and in mesic regions of Nayarit, Jalisco, Guanajuato, and Michoacán (sample 3) have significantly smaller mean total lengths than populations at higher elevations or lower latitudes. Populations on the Sierra Madre Oriental and surrounding areas in southern San Luis Potosí, northern Veracruz, and Puebla (sample 5), and in southern Veracruz (sample 6), as well as those on both the Sistema Montañoso and Sierra Madre del Sur in Oaxaca (sample 7) and the Mesa Central and surrounding areas in Chiapas (sample 8), have mean total lengths that are approximately intermediate between means of populations to the north (see above) and those of populations in eastern Chiapas and Guatemala. Of this group of montane Mexican populations, the one from Oaxaca (sample 7) has the largest mean total length. Populations in Honduras, El Salvador, and Nicaragua (sample 10) have a smaller mean total length than those at higher latitudes, thus breaking the trend of increasing size with decreasing latitude, but the population in Costa Rica and Panamá (sample 11) has a significantly larger mean total length than that (sample 10) immediately adjacent to the north. The population inhabiting easternmost Chiapas and Guatemala (sample 9) has the largest mean total length of all populations sampled, followed by that of shrews inhabiting the Valley of Mexico (sample 4).

With certain exceptions, geographic variation in length of tail and length of hind foot follow the same general pattern as that of total length. The tail is longest in specimens from Oaxaca (sample 7), Guatemala (sample 9), and the Valley of Mexico (sample 4); it is significantly longer in Oaxacan specimens (sample 7) than in specimens from east of the Isthmus of Tehuantepec in Chiapas (sample 8), but this may be due to errors in measurement or sampling. As with total length, the smallest means are those of samples 1 and 2 from the relatively arid northern regions of eastern México. Length of hind foot is not particularly variable, and demonstrates no clear pattern of variation except a slight tendency for decrease at either end of the geographic range of the species.

Geographic variation in each cranial measurement shows approximately the same general pattern, which corresponds closely with that shown by external measurements. Populations characterized by consistently having the smallest cranial dimensions are those

(samples 1, 2, and 3) in the lowlands or at middle elevations in northeastern México, on the Mexican Plateau, and in western México mostly north of the Cordillera Volcánica. The population (sample 4) inhabiting the Valley of Mexico averages only slightly larger than those (samples 1, 2, and 3) from areas farther to the north and west in every measurement except condylobasal length, which averages greater in that population than in all others except those (samples 7, 8, and 9) inhabiting extreme southern México and Guatemala. Cranial size generally increases in clinal fashion from northwest (samples 5 and 6) to southeast (sample 8) on the mountains of southern México, with the exception that cranial dimensions characteristically average slightly larger in Oaxaca (sample 7) than in adjacent populations inhabiting the Sierra Madre Oriental in southern Veracruz (sample 6) and the Mesa Central in Chiapas (sample 8). Specimens from easternmost Chiapas and Guatemala (sample 9) have the largest mean cranial dimensions of all populations studied for each measurement except one (interorbital breadth). The population from Costa Rica and Panamá (sample 11) has a larger mean interorbital breadth, length of maxillary toothrow, and length of M₂ than the adjacent population from farther to the north in Honduras, El Salvador, and Nicaragua (sample 10); the latter population, however, averages larger than the former in other cranial dimensions analyzed.

Presentation of the results of multivariate analysis of geographic variation in *C. parva* in the form of a semi-diagrammatic map with distance coefficients connecting geographically and ecologically feasible routes of gene flow among samples (Fig. 13) demonstrates certain trends alluded to by successive analyses of individual characters. First, populations in northern and western México (samples 1, 2, and 3) constitute a cohesive taxonomic unit (the subspecies *berlandieri*) that differs appreciably from all other populations to the east and south. Second, specimens from the Valley of Mexico (sample 4) differ markedly from specimens from lower elevations and higher latitudes (samples 1, 2, and 3), but do not differ appreciably in mensural characteristics from specimens representing montane populations farther to the east. Although recognition of the population inhabiting the Valley of Mexico (sample 4) as a distinct taxonomic entity solely on the basis of mensural characters would be tenuous, that population also is characterized by black pelage unlike that of any adjacent population, and therefore is considered to comprise a distinct subspecies (*soricina*).

The third feature of interest in Fig. 13 is the high distance co-

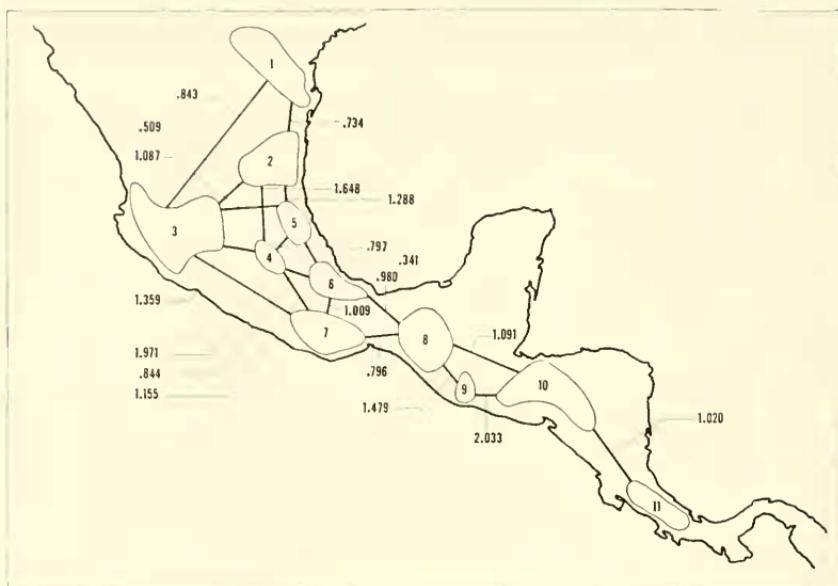
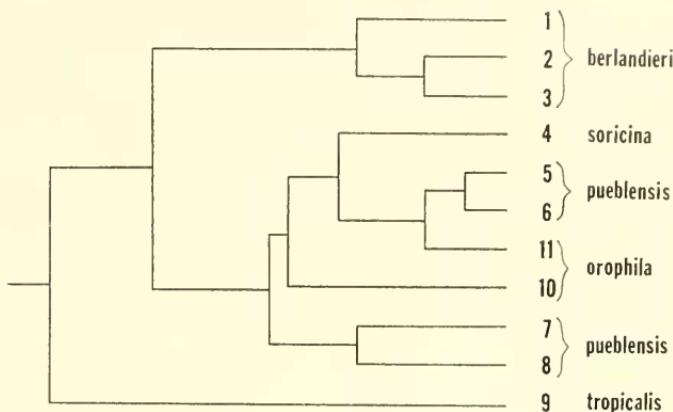


FIG. 13. Semi-diagrammatic representation of geographic relationships of samples of *Cryptotis parva*. Localities included in numbered samples are listed in Methods and Materials. Distance coefficients are illustrated for all potential routes of gene flow; the lower the coefficient, the greater the resemblance (see text).

efficient (1.009) separating the population (sample 6) on the southern part of the Sierra Madre Oriental in Veracruz from that (sample 7) in Oaxaca. One factor that probably contributed to this situation was the fact that it was necessary to lump all specimens from the state of Oaxaca, including those from both the Sistema Montañoso and the Sierra Madre del Sur, into a single sample in order to have sufficient specimens for analysis. Preliminary analysis of variability within the combined sample from Oaxaca substantiated the practicality of pooling the specimens, but the resulting distance coefficients between the Oaxacan sample and adjacent populations probably was increased thereby because of added variance within the pooled sample. Examination of a phenogram (Fig. 14) based on distance matrices demonstrates the same results in another way; samples 5 and 6 are split off from samples 7 and 8 by the interposed samples 10 and 11. The true distance coefficients and the phenogram coefficients, however, are only 78.4 per cent correlated in this instance; thus, the disparity regarding phenetic relationships may be due to numerical distortion. The basic pattern of the phenogram is informative, but it is necessary to interpret deviations from expectation based on knowledge from qualitative as well as mensural characters.

2.20 1.80 1.40 1.00 0.60 0.20



UPGA - 0.784

FIG. 14. Phenogram of numbered samples (see Fig. 13) of *Cryptotis parva* computed from distance matrices on standardized characters and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram is 0.784. Subspecific assignment is indicated to the right of the sample numbers.

In this regard, montane populations (samples 5, 6, 7, and 8) of *C. parva* from southern México share features of the dentition and have approximately the same pelage coloration; therefore, all are considered here to represent a single geographically variable subspecies (*pueblensis*).

Demarcation of the population (sample 9) in easternmost Chiapas and Guatemala as a separate subspecies (*tropicalis*) is justified by the extraordinarily high distance coefficients shown in Fig. 13, the characteristically large external and cranial dimensions of these shrews, and relatively dark color of pelage. Specimens from farther to the east and southeast (samples 10 and 11) have significantly smaller dimensions than those from easternmost Chiapas and Guatemala, and are considered to represent a fifth subspecies (*orophila*).

As discussed earlier, strict adherence to distance coefficients as the criterion for subspecific determination would necessitate nominal recognition of several populations in addition to the five recognized here. Geographic variation of qualitative characters of dentition and pelage, however, corresponds well with the division of Middle American populations of *C. parva* into only five subspecies

pending acquisition and study of additional specimens from certain critical parts of the range of the species.

***Cryptotis parva berlandieri* (Baird)**

Blarina berlandieri Baird, Mammals, in Reports of explorations and surveys . . . from the Mississippi River to the Pacific Ocean . . ., 8(1):53, 14 July 1858; Baird, Mammals of the boundary, in United States and Mexican Boundary Survey, . . ., p. 5, 1859; Merriam, N. Amer. Fauna, 10:20, 31 December 1895; Bailey, N. Amer. Fauna, 25:208, 24 October 1905.

Cryptotis parva berlandieri, Davis, Jour. Mamm., 22:413, 13 November 1941; Goodwin, Amer. Mus. Novit., 1689:3, 12 November 1954; Findley, Univ. Kansas Publ., Mus. Nat. Hist., 7:615, 10 June 1955; Booth, Walla Walla College Publ., Dept. Biol. Sci. and Biol. Sta., 20:9, 10 July 1957; Hall and Kelson, The mammals of North America, 1:57, 31 March 1959; Alvarez, Univ. Kansas Publ., Mus. Nat. Hist., 14:396, 20 May 1963.

B[larina]. b[revicauda]. berlandieri, Elliot, Field Columbian Mus. Publ. 71, Zool. Ser., 3:149, 20 March 1903.

Blarina parva, Merriam, N. Amer. Fauna, 10:18, 31 December 1895 (part).

Blarina pergracilis Elliot, Field Columbian Mus. Publ. 71, Zool. Ser., 3:149, 20 March 1903, holotype from Ocotlán, Jalisco.

Cryptotis pergracilis macer Miller, Proc. Biol. Soc. Washington, 24:223, 31 October 1911, holotype from near Guanajuato, Guanajuato; Hall and Kelson, The mammals of North America, 1:58, 31 March 1959.

Cryptotis pergracilis pergracilis, Miller, Proc. Biol. Soc. Washington, 24:223, 31 October 1911; Hall and Villa-R, Univ. Kansas Publ., Mus. Nat. Hist., 1:440, 27 December 1949; Hall and Villa-R, Anal. Inst. Biol., 21:165, 28 September 1950; Baker and Alcorn, Jour. Mamm., 34:116, February 1953; Hall and Kelson, The mammals of North America, 1:58, 31 March 1959; Hooper, Jour. Mamm., 42:121, February 1961.

Cryptotis berlandieri, Miller, Bull. U.S. Nat. Mus., 79:25, 31 December 1912.

Cryptotis pergracilis nayaritensis Jackson, Proc. Biol. Soc. Washington, 46:79, 27 April 1933, holotype from Tepic, 3000 ft., Nayarit; Hall and Kelson, The mammals of North America, 1:58, 31 March 1959.

Cryptotis pergracilis, Twente and Baker, Jour. Mamm., 32:120, February 1951; Koopman and Martin, Jour. Mamm., 40:4, February 1959.

Cryptotis pergracilis pueblensis, Dalquest, Louisiana State Univ. Studies, Biol. Sci. Ser., 1:22, 28 December 1953 (part); Goodwin, Amer. Mus. Novit., 1689:3, 12 November 1954; Hall and Kelson, The mammals of North America, 1:58, 31 March 1959 (part).

Cryptotis pergracilis macra, Miller and Kellogg, Bull. U.S. Nat. Mus., 205:39, 1955.

Cryptotis parva, Raun, Southwestern Nat., 10:214, 1 July 1965.

Lectotype.—Young, sex unknown, preserved in alcohol (juvenile pelage) with skull removed, U.S. National Museum no. 2159, probably obtained (on an unknown date) by J. L. Berlandier, but received from Lt. D. N. Couch; catalogued on 14 February 1857; type locality, vicinity of Matamoros, Tamaulipas.

Distribution.—Mesic regions along the Río Grande and its tributaries east of the Sierra Madre Oriental as far south as southern Tamaulipas, thence westward

across the Sierra Madre in mesic areas on the Mexican Plateau, and farther westward on either side of the Sierra Madre Occidental north of the Cordillera Volcánica except near the Pacific coastal lowlands, where populations extend south of the Cordillera onto the Sierra de Coaleomán in Michoacán (Fig. 12). Also known from north of the Río Grande in Texas.

Measurements of lectotype.—Length of tail 17; length of hind foot 10 (measurements taken after long immersion in alcohol).

Color.—Dorsum in winter pelage near Bister, Olive-Brown, or Buffy Brown in specimens collected after about 1940, usually nearer Sepia or Snuff Brown in specimens collected prior to that time; summer pelage paler, grayer, less reddish; juvenal pelage nearer buffy olive or gray.

Comparisons.—Specimens referred to *berlandieri* average paler and significantly smaller in most measurements (Table 1) than specimens referred to other subspecies of *C. parva* treated in this paper.

Remarks.—Baird's (1858:53) original description of *berlandieri* was based on four specimens; one (USNM 2159) was figured but none was designated as holotype. The figured specimen subsequently was designated as the lectotype by Lyon and Osgood (1909:237).

As presently understood, the range of *berlandieri* extends into southern Texas as far as Dilley, Frio County, and San Diego, Duval County (Davis, 1941:418). Raun (1965:214) reported the westernmost record for *C. parva* in the watershed of the Río Grande (from "Rancho las Rusecas," 10 mi. NE Melchor Múzquiz, about 1600 feet, Coahuila), and commented (*op. cit.*:218) on the "tenuous division of *C. parva* into subspecies." His comment probably was justified, but the name *berlandieri* here is retained pending completion of a systematic review of United States populations of *Cryptotis parva*.

Cryptotis parva berlandieri is the most highly specialized dentally of the Middle American subspecies of *C. parva*. It is also one of the most ubiquitous as regards distribution and habitat, ranging from gulf coastal lowlands to the Sierra Madre Oriental, the Mexican Plateau, and the Cordillera Volcánica, and altitudinally from just above sea level to almost 9000 feet. Because of the tolerance of *berlandieri* for varied habitats, gene flow may be almost continuous throughout its entire geographic distribution. Even so, clinal geographic variation in size and color exists among populations for which samples are available. The tendency is for individuals to grow larger and have darker pelage at higher elevations or in less xeric habitats; therefore, specimens from the Sierra Madre Oriental in southern Tamaulipas and San Luis Potosí and from the Cordillera Volcánica in Nayarit, Jalisco, and Michoacán average slightly larger

and darker than specimens from arid coastal plains or the Mexican Plateau. In most instances sample sizes were too small to permit extensive analysis of inter-populational variation of mensural characters without pooling data from several localities, but subsequent analyses of variance demonstrated that adjacent populations generally are homogeneous. Likewise, trends in variation of color from one population to the next are not abrupt.

Jackson (1933:79) named *Cryptotis pergracilis nayaritensis* on the basis of a single specimen from Tepic, Nayarit, and so far as I know that specimen remains the only representative of the genus *Cryptotis* from that state in any museum collection. The characteristics by which *nayaritensis* was distinguished from *pergracilis* (the name applied by Elliot, 1903:149, to the population of *parva* nearest Nayarit) appear to be related to age and season of capture. It is possible that acquisition and study of additional specimens from Nayarit may reveal statistically significant morphometric differences between specimens from that state and Jalisco, but the name *nayaritensis* tentatively is considered a junior subjective synonym of *berlandieri*.

Specimens examined.—143, as follows: TEXAS: VAL VERDE COUNTY: Del Rio, *ca.* 1050 ft., (not plotted), 1 (USNM); CAMERON COUNTY: Brownsville, 30 ft., 11 (1 BMNH, 10 USNM). COAHUILA: 10 mi. NE Melchor Múzquiz, *ca.* 1600 ft., 1 (TNHC). TAMAULIPAS: Camargo, 200 ft., 1 (USNM); Matamoros, 30 ft., 7 (USNM); Río Corona, 19 mi. E Cd. Victoria, *ca.* 500 ft., 2 (MCZ); 2 mi. S, 10 mi. W Piedra, 1200 ft., 1 (KU); Aserradero del Paraíso, cave 11 mi. W Gómez Fariás, *ca.* 1400 ft., 3 (1 AMNH, $\frac{1}{2}$ AMNH); 6 mi. N Rancho del Tigre, *ca.* 4 mi. N Ocampo, 3400 ft., 6 (AMNH); 1 mi. S Altamira, *ca.* 75 ft., 8 (KU). SAN LUIS POTOSÍ: El Salto, *ca.* 2000 ft., 4 (AMNH); 10 km. E Platamito, *ca.* 3000 ft., 3 (LSU); Alvarez, 7300 ft., 1 (MCZ). NAYARIT: Tepic, 3100 ft., 1 (USNM). JALISCO: 21 mi. SW Guadalajara, $\frac{1}{2}$ 28 (KU); $\frac{3}{2}$ mi. N Mascota, 6150 ft., 1 (KU); Huásca, *ca.* 6600 ft., 1 (ENCB); Ocotlán, 5000 ft., 4 (1 FMNH, 3 USNM); 1 mi. S Ocotlán, 5000 ft., 3 (KU). GUANAJUATO: Guanajuato, *ca.* 6600 ft., 1 (USNM). MICHOACÁN: 1 km. S Cumuato, 4900 ft., 1 (LACM); *Colonia Ibarra*, *ca.* 7200 ft., 3 (1 MVZ, 2 UNAM); *La Palma*, 4250 ft., 3 (LACM); 2 mi. E *La Palma*, *ca.* 4300 ft., $\frac{1}{2}$ 39 (KU); 7 km. NNW Quíroga, *ca.* 5900 ft., 3 (USNM); 3 mi. E Pátzcuaro, 7200-8000 ft., 1 (UMMZ); 12 km. W Morelia, *ca.* 6600 ft., 4 (UNAM); "1 hr. 20 min. [by mule] NE Rancho Baralosa" (Hooper, 1961:120-121), 8900 ft., 1 (UMMZ).

Cryptotis parva orophila (J. A. Allen)

Blarina (Soriciscus) orophila J. A. Allen, Bull. Amer. Mus. Nat. Hist., 7:340, 8 November 1895.

Blarina olivaceus J. A. Allen, Bull. Amer. Mus. Nat. Hist., 24:669, 13 October 1908, holotype from San Raphael del Norte, 5000 ft., Jinotega, Nicaragua.

Cryptotis olivaceus, Miller, Bull. U.S. Nat. Mus., 79:26, 31 December 1912.

Cryptotis micrura, Goodwin, Bull. Amer. Mus. Nat. Hist., 79:116, 29 May 1942; Harris, Occas. Papers Mus. Zool., Univ. Michigan, 476:7, 8 October 1943; Hall and Kelson, The mammals of North America, 1:63, 31 March 1959 (part).

Cryptotis orophila, Goodwin, Bull. Amer. Mus. Nat. Hist., 87:289, 31 December 1946; Hall and Kelson, The mammals of North America, 1:64, 31 March 1959.

Cryptotis olivacea, Hall and Kelson, The mammals of North America, 1:62, 31 March 1959.

Holotype.—Subadult, sex unknown, skin (adult winter pelage) and skull, originally in alcohol, American Museum of Natural History no. 9640/9558, obtained in February of 1894 by G. K. Cherrie; type locality, "Irazú Range," Cartago, Costa Rica.

Distribution.—Mesic highlands of Honduras, El Salvador, Nicaragua, Costa Rica, and at least westernmost Panamá (Fig. 12).

Measurements of holotype.—Palatal length 7.6; maxillary breadth 5.4; interorbital breadth 4.1; length of maxillary toothrow 6.5; length of M2 1.3.

Color.—Dorsum in winter pelage near Clove Brown in Costa Rican populations sampled in 1946, as dark as Mummy Brown or near Chaetura Black or Fuscous in specimens from Panamá collected in 1946 and 1962, nearer Bister in a specimen from Costa Rica obtained in 1894; dorsum in summer pelage Bister in specimens obtained in Costa Rica in 1946, nearer Olive-Brown in specimen obtained in Nicaragua in 1908; dorsum in juvenal pelage "salt-and-pepper" gray; venter always conspicuously paler than dorsum, hairs usually tipped with white or pale buff regardless of season or degree of foxing.

Comparisons.—Comparison with *C. p. berlandieri* is given in the account of that subspecies. From *C. p. soricina*, all but the southernmost populations of *C. p. orophila* differ in having paler dorsal pelage. From *C. p. pueblensis*, *C. p. orophila* differs in having darker pelage and significantly smaller external and cranial dimensions (Table 1). From *C. p. tropicalis*, *C. p. orophila* differs in having substantially smaller external and cranial dimensions (Table 1).

Remarks.—*Cryptotis parva orophila* is a wide-ranging, geographically and altitudinally variable subspecies that, nevertheless, apparently represents a genetically cohesive assemblage of populations. Morphological divergence resulting from lack of, or decreased, gene flow across the "Nicaraguan gap" is minimal, specimens to the south having slightly darker dorsal pelage. This trend, however, is already established in populations both to the north and south of the "gap," and is not considered to represent a "step" comparable to others that make up the step-cline of geographic variation among subspecies of *C. parva*. Likewise, mensural characteristics of Honduran and Costa Rican populations of *orophila* differ slightly, but the difference is not of comparable degree of magnitude to those that distinguish subspecies in México, even though a gap of more than 200 miles exists across southern Nicaragua from which no specimens as yet have been obtained. It appears, therefore, that if gene flow is interrupted between Honduras and Costa Rica, the interruption has not been of sufficient duration to foster recognizable

subspecies. Isolated populations of this species probably occur on the remaining forested highlands of Nicaragua, and the apparent gap in distribution could be due to insufficient sampling or the Recent destruction by man of suitable habitat for the shrews, or both.

The holotype of *orophila* is a subadult in foxed winter pelage, whereas the holotype and paratype of *Blarina olivaceus* J. A. Allen are in summer and juvenal pelages, respectively. The differences used by Allen (1908:669) to distinguish between the two taxa apparently are due to maturative and seasonal variation rather than genetic divergence.

The holotype of *orophila* was reported by J. A. Allen (1895:340) to have been obtained by George K. Cherrie on Volcán Irazú. Goodwin (1944:2) amended the type locality to "Irazú Range" to correspond to the locality recorded on the label of the holotype, and to coincide with his belief that the specimen "was taken probably nearer the foothills of Volcán Irazú than the upper slopes as has generally been supposed."

A single individual (AMNH 14847) of *orophila* was obtained on 20 June 1895 by Anastasio Alfaro at a place recorded on the specimen label as "La Estrella," Costa Rica. This locality was interpreted by Goodwin (1946:289) to be "a small village on the Estrella River, 6 miles inland from the Caribbean coast and 18 miles south of Limón." Although this interpretation may be correct, it seems more likely to me that the site of capture was the village of Estrella in Cartago Province, which is situated at an elevation of between 6000 and 7000 feet, and from which an additional specimen of *orophila* (UMMZ 64147) was obtained in humid subtropical habitat in 1931.

Specimens examined.—37, as follows: HONDURAS: Lago de Yojóa, ca. 2500 ft., 1 (MCZ); Belén, ca. 5200 ft., 1 (AMNH); Cerro Cantoral, ca. 5500 ft., 1 (AMNH); Montserrat Cloud Forest, near Yuscarán, ca. 5000 ft., 2 (MCZ). EL SALVADOR: Cerro Montecristo, 2 (USNM). NICARAGUA: San Raphael del Norte, 5000 ft., 2 (AMNH); Santa María de Ostuma, 4000 ft., 2 (UMMZ). COSTA RICA: Cinchona, ca. 5200 ft., 1 (KU); Zarcero, ca. 6000 ft., 1 (FMNH); "Irazú Range," 1 (AMNH); *Finca Coliblanca*, ca. 7750 ft., 2 (KU); *San José*, ca. 3800 ft., 1 (USNM); *San Pedro Montes de Oca*, 4040 ft., 1 (AMNH); *Estrella*, 6000-7000 ft., 1 (UMMZ); "La Estrella" (of A. Alfaro), 1 (AMNH); *Cartago*, 4700-4750 ft., 2 (1 KU, 1 UMMZ); *Cerro Tablazo*, ca. 5000 ft., 1 (USNM); *Río Navarro*, *El Muñeco*, 3800-4500 ft., 3 (UMMZ); "Guarco," 1 (KU); *Monte Verde*, 7 (UMMZ). PANAMÁ: *Santa Clara*, 3600-4200 ft., 2 (USNM); *Cerro Punta-Boquete trail*, 6800 ft., 1 (USNM).

Cryptotis parva pueblensis Jackson

Cryptotis pergracilis pueblensis Jackson, Proc. Biol. Soc. Washington, 46:79, 27 April 1933; Hall and Kelson, The mammals of North America, 1:58, 31 March 1959 (part).

Blarina tropicalis Merriam, N. Amer. Fauna, 10:22, 31 December 1895 (part). *Cryptotis parva berlandieri*, Davis, Jour. Mamm., 25:376, 12 December 1944.

Cryptotis micrura, Hooper, Jour. Mamm., 28:43, February 1947; Villa-R, Anal. Inst. Biol., 19:498, 30 June 1949; Findley, Univ. Kansas Publ., Mus. Nat. Hist., 7:616, 10 June 1955; Hall and Kelson, The mammals of North America, 1:63, 31 March 1959 (part); Hall and Dalquest, Univ. Kansas Publ., Mus. Nat. Hist., 14:207, 20 May 1963.

Cryptotis celatus Goodwin, Amer. Mus. Novit., 1791:1, 28 September 1956, holotype from Las Cuevas, Santiago Lachiquiri, Tehuantepec, Oaxaca; Hall and Kelson, The mammals of North America, 1:58, 31 March 1959; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:41, 30 April 1969.

Holotype.—Subadult male, skin (adult winter pelage) and skull, U.S. National Museum no. 92720, obtained on 6 January 1898 by E. A. Goldman, original number 12014; type locality, Huauchinango, about 5000 ft., Puebla.

Distribution.—Sierra Madre Oriental and surrounding mesic regions of southern San Luis Potosí, Veracruz, Hidalgo, and Puebla; hence southward on the Sistema Montañoso and the Sierra Madre del Sur in Oaxaca, and across the Isthmus of Tehuantepec onto the Mesa Central and Sierra Madre of Chiapas (Fig. 12).

Measurements of holotype.—Total length 85; length of tail 22; length of hind foot 13; condylobasal length 16.1; palatal length 6.7; maxillary breadth 5.3; interorbital breadth 3.9; length of maxillary toothrow 6.2; cranial breadth 8.3; length of M2 1.3.

Color.—Dorsum in winter pelage near Sepia or Bister in most specimens collected in 1895, 1947, and 1949, but sometimes nearer Mummy Brown or Olive-Brown; dorsum in summer pelage near Sepia or Olive-Brown in specimens collected in 1893-1895, nearer Clove Brown in specimens collected in 1966; dorsum in juvenal pelage near Fuscos or Chaetura Drab in specimens collected in 1893 and 1895, darker than Fuscos (nearer Olive-Brown or Bister) in specimens collected in 1947.

Remarks.—*Cryptotis parva pueblensis* is primarily an inhabitant of highland or mid-elevation forests and savannas, although a few specimens referable to that subspecies have been collected from just above sea level in the gulf coastal lowlands. Specimens from lowland localities tend to be paler and smaller (in this respect resembling *berlandieri*) than more nearly typical specimens from higher elevations; intergradation with *berlandieri* thus occurs throughout southern Tamaulipas, southeastern San Luis Potosí, and northern Veracruz and Puebla, and seemingly is correlated (although no statistical tests were made) with elevation. Consequently, specimens from Boca del Río and Catemaco, in the lowlands of coastal Veracruz, reasonably could be referred to *berlandieri* rather than to *pueblensis*, but to do so would necessitate including the coastal lowlands of eastern México as far south as the Isthmus of Tehuantepec within the range of *berlandieri* (see also Davis, 1944:376, and Findley, 1955a:615-616). It seems to me that a more tenable

alternative is to recognize that color and size in *C. parva* vary altitudinally in eastern México, and to restrict the name *berlandieri* to apparently interbreeding populations in southern Texas and northern México rather than geographically disjunct (and therefore non-interbreeding) but phenetically similar populations.

The Isthmus of Tehuantepec apparently does not serve as a barrier to gene flow in *C. parva*, as no significant differences in size or color exist between populations in Oaxaca and Chiapas. A specimen (AMNH 145838) from the isthmus is slightly paler and smaller than those on either side of the isthmus, and was given the name *Cryptotis celatus* by Goodwin (1956:1). Local or individual variation in what may prove to be suboptimal habitat for the species, however, does not necessarily reflect biological relationships, and in my opinion does not warrant formal recognition at the subspecific level. Clinal variation in size is prevalent throughout the range of the subspecies, external and cranial size gradually increasing from populations in Veracruz to those in Oaxaca and Chiapas, and terminating in Guatemala in a recognizable subspecies (*C. p. tropicalis*). There are no obvious breaks in the cline throughout the distribution of *pueblensis* that approach the magnitude, for example, of the break between *pueblensis* and *tropicalis*.

Specimens examined.—1085, as follows: SAN LUIS POTOSÍ: 15 km. NE Xilitla, 1 (LSU); 3 km. NE Xilitla, ca. 2200 ft., 2 (LSU); Xilitla, ca. 2200 ft., 1 (LSU); 2 mi. E Xilitla, ca. 3000 ft., 1 (UMMZ); 2 km. SW Huichihuayán, ca. 400 ft., 1 (LSU). VERACRUZ: 7 km. W El Brinco, 800 ft., 1 (KU); 5 km. N Jalapa, 4500 ft., 1 (KU); 1½ mi. N Jalapa, 4500 ft., 1 (UMMZ); Xico, 4800-6500 ft., 8 (USNM); 7 km. NNW Cerro Gordo, 1500 ft., 3 (KU); Teocelo, 4500-5000 ft., 11 (3 KU, 8 MCZ); Mirador, 3800 ft., 3 (USNM); Boca del Rio, ca. 30 ft., 1 (TCWC); 11 km. E Mecayucan, 200 ft., 1 (KU); Potrera Vieja, 1700 ft., 1 (KU); Orizaba, 4000-4200 ft., 6 (USNM); Catemaco, 1000-1500 ft., 1 (USNM). PUEBLA: Metlaltoyuca, 800 ft., 1 (USNM); Villa Juárez, 3300 ft., 1 (ENCB); Huauchinango, ca. 5000 ft., 5 (1 UMMZ, 4 USNM). OAXACA: Teotitlán del Camino, ca. 3000 ft., 1 (AMNH); Tuxtepec, 300 ft., 1 (USNM); Choapan, 2800-3000 ft., 1 (USNM); approx. 5 mi. NE Putla (km. 123), 4350 ft., 1 (CAS); Santiago Lachiquirí, ca. 4900 ft., 1 (AMNH); 20 mi. S, 4 mi. E Sola de Vega, 4800 ft., 1 (KU); Sta. Catarina Juguila, 5000 ft., 7 (USNM); 4 km. W San Gabriel Mixtepec, 2500 ft., 2 (CAS); 2 mi. E San Gabriel Mixtepec, ca. 3500 ft., 1 (AMNH); approx. 6 mi. N Puerto Escondido (km. 212), 2400 ft., 1 (CAS); Río Jalatengo, approx. 3 mi. SW San Miguel Suchixtepec (km. 178), 4275 ft., 2 (CAS); San Agustín Loxicha, ca. 6600 ft., 1 (AMNH); Pluma Hidalgo, 3000-4700 ft., 2 (USNM). CHIAPAS: Yajalón, 3000 ft., 1 (USNM); 1 mi. S Pueblo Nuevo Solistahuacán, 5700 ft., 1 (KU); Río Pulucum, NE Bochil, ca. 4560 ft., 1 (UNAM); 8 6/10 mi. SW San Cristóbal de las Casas, 7800 ft., 2 (CAS); Volcán Kagchiná, 3½ km. N Las Margaritas, ca. 4900 ft., *174 (JDS); Cucva Los Llanos, 9 km. S Las Margaritas, ca. 4900 ft., *828 (JDS); valley of Comitán, 5700 ft., 1 (USNM); Villa Flores, ca. 2000 ft., 1 (UMMZ); Prusia, ca. 3300 ft., 1 (UMMZ); Finca Esperanza, 4 mi. NE Esquitla, ca. 500 ft., 1 (UMMZ); Huixtla, ca. 4600 ft., 1 (UNAM).

Additional record.—CHIAPAS: Finca Prusia, ca. 3650 ft. (Villa, 1949:498).

Cryptotis parva soricina (Merriam)

Blarina soricina Merriam, N. Amer. Fauna, 10:22, 31 December 1895.

Blarina berlandieri, Alston, Biologia Centrali-Americanana. Mammalia, p. 208, 1879-1882 (part).

C[ryptotis]. *soricina*, Miller, Proc. Biol. Soc. Washington, 24:221, 31 October 1911.

Cryptotis soricina, Villa-R, Anal. Inst. Biol., 23:320, 20 May 1953; Hall and Kelson, The mammals of North America, 1:63, 31 March 1959.

Holotype.—Adnl male, skin (adult winter pelage) and sknll, U.S. National Museum no. 50762, obtained on 5 December 1892 by E. W. Nelson, original number 3989; type locality, Tlalpan, 7600 ft., Distrito Federal.

Distribution.—Apparently confined to the Valley of Mexico in the Estado de México and Distrito Federal (Fig. 12).

Measurements of holotype.—Total length 88; length of tail 23.5; length of hind foot 12.5; condylobasal length 17.2; palatal length 7.3; maxillary breadth 5.0; interorbital breadth 3.7; length of maxillary toothrow 6.2; cranial breadth 8.4; length of M2 1.2.

Color.—Dorsum in winter pelage blackish, darker than Mummy Brown in specimens collected in 1892 and 1899.

Comparisons.—From the geographically contiguous subspecies, *C. p. berlandieri* and *C. p. pueblensis*, *C. p. soricina* differs most conspicuously in having darker dorsal pelage.

Remarks.—All of the specimens of *soricina* presently available in museum collections were obtained at the southern end of the Valley of Mexico (see also Villa-R, 1953). Probably the subspecies had a much more extensive geographic range prior to drainage and regulation of Lake Texcoco, the Xochimilco-Chaleo lake system, and the ground waters associated with the springs of Chapultepec and the island capital of Tenochtitlan. There is convincing evidence (Meek, 1904) based on the distribution of certain fishes that the drainage system of the Valley of Mexico at some time in the Pleistocene was part of the Altiplanicie Meridional, which supposedly extended from the Valley of Mexico to Jalisco and was drained by the Río Lerma (Tamayo, 1964:109). If such a hydrographic system actually existed during the late Pleistocene, this would have provided a suitable route of dispersal to the Valley of Mexico from Jalisco, and subsequent drainage would have provided the reduced gene flow necessary for subspeciation.

Specimens assignable to *berlandieri* from the Cordillera Volcánica, especially those from localities in Michoacán (Pátzcuaro and Morelia) nearest the range of *soricina*, are larger and darker than typical *berlandieri*. Intergradation with *soricina* in mensural (but

not pelage) characteristics is suggested by variation seen in specimens of *pueblensis* from the vicinity of Orizaba, Veracruz.

Specimens examined.—63, as follows: ESTADO DE MÉXICO: 1 km. S San Juan Zitaltepec, ca. 4100 ft., 1 (ENCB); Tlapacoyán, ca. 7200 ft., 58 (1 ENCB, *57 ENCB). DISTRITO FEDERAL: Bosque Chapultepec, 7400 ft., 1 (UNAM); Tlalpan, ca. 7600 ft., 3 (1 BMNH, 2 USNM).

Cryptotis parva tropicalis (Merriam)

Blarina tropicalis Merriam, N. Amer. Fauna, 10:21, 31 December 1895 (*part*), a renaming of *Sorex micrurus* Tomes, preoccupied.

Corsira tropicalis Gray, Proc. Zool. Soc. London, p. 79, 1843 (*nomen nudum*).

Sorex micrurus Tomes, Proc. Zool. Soc. London, 1861:279, 1862, lectotype (informally designated by Thomas—see Handley and Choate, 1970) from Cobán, about 4400 ft., Alta Verapaz, Guatemala. Not *Galemys*. *micrurus* Pomel, Arch. Sci. Phys. Nat. (Geneva), 9:249, 1848 [= *Sorex talpoides* Gapper].

Blarina micrura, Alston, Proc. Zool. Soc. London, p. 445, 1877.

Cryptotis. *tropicalis*, Miller, Proc. Biol. Soc. Washington, 24:221, 31 October 1911.

Cryptotis micrura, Miller, Bull. U.S. Nat. Mus., 128:32, 1924 (*part*); Goodwin, Bull. Amer. Mus. Nat. Hist., 68:5, 12 December 1934; Murie, Misc. Publ. Mus. Zool., Univ. Michigan, 26:17, 15 July 1935 (*part*); Hall and Kelson, The mammals of North America, 1:63, 31 March 1959 (*part*).

Cryptotis tropicalis, Handley and Choate, Proc. Biol. Soc. Washington, 83:200, 27 May 1970.

Lectotype.—Young or subadult, sex unknown, British Museum (Natural History) no. 7.1.1.33, obtained in 1859 by O. Salvin and L. Fraser, original number 2778 (of Fraser); type locality, Cobán, about 4400 ft., Alta Verapaz, Guatemala.

Distribution.—Mesa Central and Sierra Madre of easternmost Chiapas, and highlands of Guatemala and British Honduras (Fig. 12).

Measurements of holotype.—None available.

Color.—Dorsum in winter pelage darker than Olive-Brown, near Sepia in specimen obtained in 1925; “salt-and-pepper” brown, almost Olive-Brown in summer and juvenal pelages of specimens collected in 1926; venter tipped with white or buff.

Comparisons.—*Cryptotis parva tropicalis* differs most conspicuously from all other subspecies of *C. parva* by its large external and cranial size (Table 1).

Remarks.—Handley and Choate (1970) summarized the nomenclatorial history of the Guatemalan shrew and gave reasons for use of the name *tropicalis* rather than *micrurus* for the taxon. It is regrettable that all of the specimens excepting the holotype that were referred by Merriam (1895:22) to *tropicalis* now are assigned to another subspecies (*pueblensis*), but, in accordance with the Code of Zoological Nomenclature, *tropicalis* remains the valid name for the Guatemalan shrew.

When Merriam (*op. cit.*:21) in effect elevated the name *tropicalis* from the status of a *nomen nudum* to the valid name for the Guatemalan shrew, he referred to "the two original type specimens" but failed to designate a type. As pointed out by Handley and Choate (*op. cit.*), Oldfield Thomas selected and labeled a specimen (BMNH 7.1.1.33) from the type series as "co-type and lectotype." Formal designation of that specimen as lectotype, however, must date from the present paper. The type locality was given by Tomes (1862:279) as Dueñas, Guatemala. Alston (1879:56), however, later indicated that the specimens (actually three) that comprised the type series had been obtained near Cobán rather than at Dueñas.

Cryptotis parva tropicalis apparently intergrades with *C. p. pueblensis* to the northwest and *C. p. orophila* to the east. Judging by specimens presently in collections, the change both in color and size between *pueblensis* and *tropicalis* is abrupt; specimens of the former from near Comitán, Finca Esperanza, and Las Margaritas, Chiapas, show no indication of intergradation of mensural characteristics, and clearly are referable to *pueblensis* on the basis of their relatively pale dorsal coloration and small size. Intergradation with *orophila*, however, is more clearly demonstrated by specimens at hand; specimens referred to *orophila* from western El Salvador and Honduras are as dark as *tropicalis* but are conspicuously smaller, thus distinction between these subspecies, at least with specimens presently available, can readily be made in almost every instance solely on the basis of standard external measurements.

Four specimens (UMMZ 63008-11) from Mountain Pine Ridge, British Honduras, provisionally referred herein to *tropicalis* are paler and slightly smaller than typical specimens from Guatemala. Their external and cranial dimensions approach those that would be expected of intergrades between *tropicalis* and *orophila* (although more closely resembling the former), whereas the color of pelage is paler than in either of those taxa and resembles that of *pueblensis*. Assignment to *tropicalis* is based on similarity of cranial dimensions and on geographic grounds; acquisition and study of additional specimens may reveal either that populations from damp, forested regions of the Yucatan Peninsula comprise an unnamed subspecies or that a gradual cline of decreasing size and pelage pigmentation extends from the mountains of southern Guatemala northward onto the Yucatan Peninsula.

Specimens examined.—24, as follows: CHIAPAS: La Libertad, *ca.* 3640 ft., 2 (UNAM); Unión Juárez, *ca.* 4000 ft., 1 (UNAM). BRITISH HONDURAS: Mountain Pine Ridge, 12 mi. (by road) S Cayo, 1000 ft., 4 (UMMZ). GUATEMALA: Cobán, *ca.* 4400 ft., 7 (BMNH); La Primavera, 3200 ft., 1

(AMNH); Finca La Paz, ca. 4900 ft., 2 (UMMZ); Panajachel, 4900 ft., 7 (AMNH).

Cryptotis nigrescens
(*Synonymy under subspecies*)

Distribution.—One population apparently isolated in the Balsas Basin in north-central Guerrero. Otherwise, occurs throughout tropical lowlands on the Yucatan Peninsula, but at progressively higher elevations at lower latitudes on the Mesa Central in Chiapas at least as far west as Las Margaritas, on highlands of Guatemala, El Salvador, and western Honduras, on the Cordillera de Guanacaste, Cordillera Central, and Cordillera de Talamanea in Costa Rica, in the Chiriquí region of Panamá, and on the highlands of Darién, Panamá (Fig. 15); possibly also occurs on the highlands of north-central Nicaragua.

Diagnosis.—External characteristics: size small to medium for the genus (Table 1); tail relatively short, averaging 37-41 per cent of length of head and body; front feet and claws small; juvenal and adult summer pelages often practically indistinguishable, overall appearance "salt-and-pepper" gray; adult winter pelage distinctive, almost never luxuriant although a few vermiculations sometimes present, not unlike summer pelage of other species in physical characteristics of individual hairs, overall appearance "salt-and-pepper" brown or brownish black (precise color determinations are given in accounts of subspecies).

Cranial characteristics: rostrum relatively short; braincase not especially angular; anterior limit of zygomatic plate varying from slightly anterior to mesostyle of M1 to slightly posterior of that point; posterior limit of zygomatic plate usually at level of, or posterior to, maxillary process, and above or slightly anterior to M3; dentition decidedly bulbous; anterior element of ectoloph of M1 not reduced relative to posterior element; posterior surfaces of P4-M2 not at all recessed; protoconal basin of M1 not reduced relative to hypoconal basin; M3 consisting only of paracrista and precentrorista; talonid of m3 elongate and unspecialized, but consisting only of hypoconid.

Comparisons.—Comparisons with *C. endersi*, *C. gracilis*, *C. goodwini*, and *C. parva* are given in the accounts of those species.

From *C. mexicana*, *C. nigrescens* differs as follows: pelage paler (in region of potential sympatry); braincase less angular; zygomatic plate situated slightly farther anteriorly; dentition decidedly bulbous; metacone lacking on M3; entoconid never present on talonid of m3.

From *C. goldmani*, *C. nigrescens* differs as follows: size smaller, both externally and cranially (Table 1); front feet and claws markedly smaller; rostrum relatively and actually shorter; braincase less angular; dentition decidedly bulbous; anterior element of ectoloph of M1 not reduced relative to posterior element; posterior surfaces of P4-M2 not recessed; protoconal basin of M1 not reduced relative to hypoconal basin.

From *C. magna*, *C. nigrescens* differs as follows: size markedly smaller, both externally and cranially (Table 1); tail relatively and actually much shorter, averaging 37-41 (as opposed to 52) per cent of length of head and body; braincase less angular; anterior element of ectoloph not reduced relative to posterior element (slightly reduced in *magna*); talonid of m3 consisting only of hypoconid (consisting of hypoconid and well-developed entoconid in *magna*).



FIG. 15. Geographic distribution of *Cryptotis nigrescens*. Solid circles, *C. nigrescens mayensis*; open circles, *C. nigrescens merriami* (open square, unverified literature record for *C. nigrescens merriami*); circles half black above, *C. nigrescens nigrescens*.

Remarks.—The most outstanding feature of *C. nigrescens* is its decidedly bulbous dentition. No other Recent species of *Cryptotis*, even those characterized by relatively bulbous teeth (*magna* and *endersi*), can compare with *nigrescens* as regards size of teeth relative to size of skull. Robustness of dentition is geographically variable in populations of *nigrescens*, ranging from smallest in Panamá and Costa Rica to largest on the Yucatan Peninsula, but even those individuals of *nigrescens* having the minimal expression of this characteristic can be distinguished from all other Recent species of the genus *Cryptotis* solely on the basis of their bulbous dentition.

Although *nigrescens* is known from habitats that approach the ecological extremes exhibited by populations of *parva*, individual populations of the former appear less ubiquitous in distribution than those of the latter. Moreover, on the basis of numbers of specimens available in collections it would appear that *nigrescens* is less abundant in suitable habitats than is *parva*. However, the secretive habits of *nigrescens* may render that species relatively immune to capture by commonly employed trapping methods. The advent of widespread use of pitfalls as traps for shrews may result in substantial contributions to the knowledge of these elusive mammals. Murie

(1935:17) reported that "A vase found in the [Mayan] ruins of Uaxactún [in northern Guatemala] contained skeletal remains of one hundred and four of these shrews as determined by counting the mandibles, which were quite well preserved. The vase may have formed a natural trap for the shrews, or possibly they were placed there by the Mayas as part of some ceremony." Likewise, remains of *nigrescens* frequently are found in owl pellets or in cave deposits that resulted from deterioration of owl pellets—for example, see records reported herein from Guerrero and from Volcán Kagchiná and Cueva Los Llanos, Chiapas, as well as published records (Hatt, *et al.*, 1953:59-60) from Yueatán. These data probably indicate that the paucity of wild-taken specimens does not necessarily reflect lack of abundance of individuals of the species in suitable habitats, but rather a lack of understanding of the habits and ecological requirements of the species.

The specimens of *mayensis* from Mayan ruins at Uaxactún, Guatemala, that were reported on by Murie (*loc. cit.*) were listed as *Cryptotis micrura* (Tomes), as were four shrews caught on Mountain Pine Ridge in British Honduras. I consider the latter to represent *C. parva tropicalis*.

Elevations and habitats at which specimens of *nigrescens* presently available have been collected vary as follows: 75-200 feet in habitats ranging from arid tropical scrub forest to rainforest on the Yucatan Peninsula; 2100 feet in deciduous thorn scrub forest in the Balsas Basin of Guerrero; 4900 feet in xeric scrub oak forest interspersed with savanna on the Mesa Central of Chiapas; 3200-5400 feet in relatively arid, shrubby forest of pine, oak, and alder in Guatemala; 3500-4000 feet in pine-oak forests in Honduras and El Salvador; 4500-9400 feet in evergreen, tropical deciduous, and oak cloud forests on the cordilleras of Costa Rica and Panamá.

Data on times of reproduction and molt in *nigrescens* are insufficient to permit interpretation, even when all populations are considered together. Specimens judged to be young and in juvenal pelage have been collected from January through March and in August, subadults in January, February, and August, and adults in May, October, and December. Specimens in winter pelage have been collected from December through February, whereas specimens obviously in summer pelage are known only from August. Two females (USNM 337968-69) that were obtained on Cerro Tacareuna, Panamá, in March of 1964, and that were judged to be young on the basis of unworn teeth and juvenal pelage, were recorded as "lac-

tating" by the collector, as was another young female (USNM 337966) caught in February of the same year on Cerro Malí, Panamá.

Geographic variation.—Meaningful analysis of geographic variation in *Cryptotis nigrescens* is not possible at present owing to the absence of sufficient series of specimens. Thus, the following description is based on statistical analyses of variation in only four samples representing the distribution of the species throughout Central America from the Isthmus of Tehuantepec to the Colombian border.

Cryptotis nigrescens evidently does not exhibit extensive geographic variation; analysis of variance for three measurements (maxillary breadth, length of maxillary toothrow, and length of M2) revealed no significant differences among samples. In every other measurement studied, however, specimens from the highlands of eastern Chiapas, Guatemala, Honduras, and El Salvador (sample 2) averaged larger than those of each of the other samples; with regard to palatal length, the difference was significant, and involved little overlap. The basic pattern of variation of mensural characters, as estimated on the basis of the few specimens presently available, is as follows: specimens from lowlands on the Yucatan Peninsula (sample 1) have small external and cranial dimensions; specimens from the highlands of eastern Chiapas, Guatemala, Honduras, and El Salvador (sample 2) are relatively large; specimens from the cordilleras of Costa Rica and the Chiriquí region of Panamá (sample 3), as well as those from the highlands of Darién, Panamá (sample 4), have external and cranial dimensions comparable to those of specimens from the Yucatan Peninsula (sample 1).

Distance coefficients (Fig. 16) derived from simultaneous consideration of all mensural characters further illustrates the linear geographic trend in variation. The population inhabiting the highlands of Guatemala and surrounding areas (sample 2) is separated from the population on the Yucatan Peninsula (sample 1) by a distance coefficient of 1.333; likewise, the coefficient between the former population (sample 2) and the population (sample 3) inhabiting the cordilleras of Costa Rica and Panamá is 1.509. In contrast, the distance coefficient between the population on the Yucatan Peninsula (sample 1) and the population on the cordilleras (sample 3) is only .678. The population inhabiting the cordilleras (sample 3) is separated from that inhabiting the highlands of Darién, Panamá (sample 4), by a coefficient of only .587. These data clearly demonstrate the tendency for corresponding decrease in size at either end of the geographic distribution of the species.

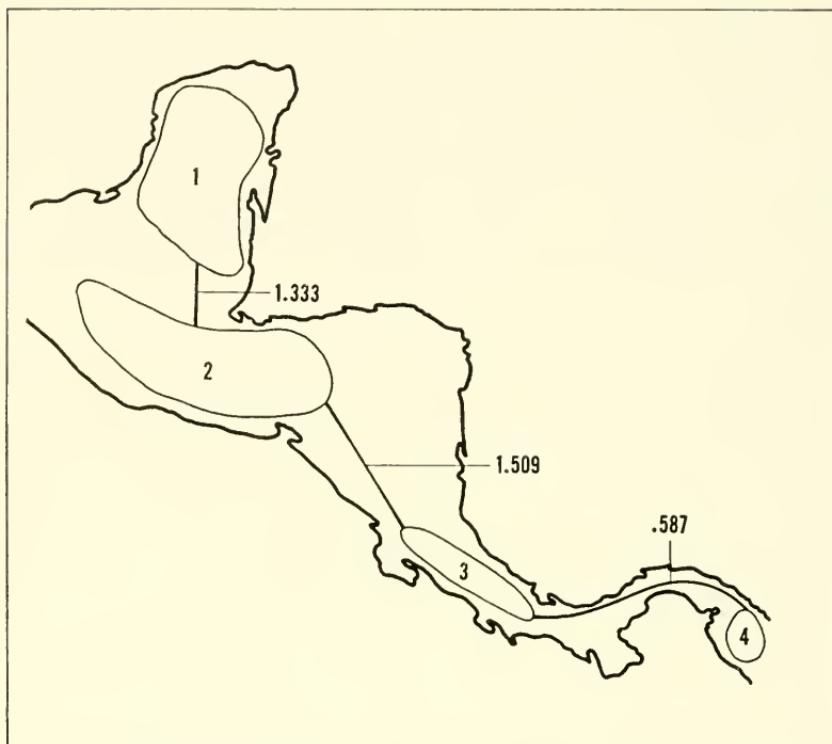


FIG. 16. Semi-diagrammatic representation of geographic relationships of samples of *Cryptotis nigrescens*. Localities included in numbered samples are listed in Methods and Materials. Distance coefficients are illustrated for all potential routes of gene flow; the lower the coefficient, the greater the resemblance (see text).

Coloration of pelage is approximately clinal in variation, ranging from pale grayish brown on the Yucatan Peninsula to almost black in Costa Rica and Panamá. The bulbous nature of the dentition apparently also is clinal, ranging from most bulbous on the Yucatan Peninsula to least bulbous in Costa Rica and Panamá. Other cranial and dental characters show no clear patterns of variation in specimens presently available.

A phenogram (Fig. 17) prepared from distance matrices demonstrates the variation of *C. nigrescens* as representing three taxonomic entities, as follows: specimens from the Yucatan Peninsula (sample 1) are considered to represent one subspecies (*mayensis*); the two samples (3 and 4) from Costa Rica and Panamá are practically indistinguishable, and are considered to represent a second subspecies (*nigrescens*); and specimens from the intervening highlands of northwestern Central America (sample 2) are considered to pertain to a third subspecies, herein described as new.

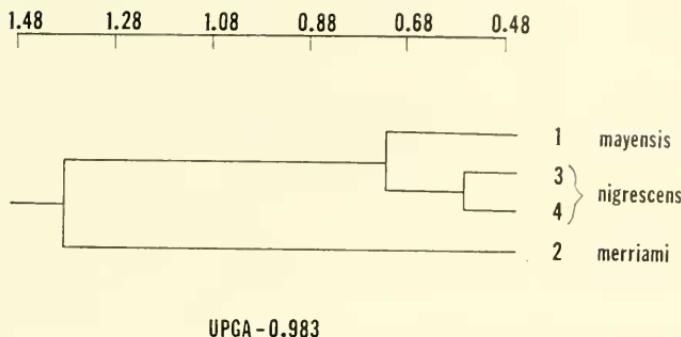


FIG. 17. Phenogram of numbered samples (see Fig. 16) of *Cryptotis nigrescens* computed from distance matrices on standardized characters and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram is 0.983. Subspecific assignment is indicated to the right of the sample numbers.

Cryptotis nigrescens mayensis (Merriam)

Blarina mayensis Merriam, Proc. Washington Acad. Sci., 3:559, 29 November 1901.

Cryptotis mayensis, Miller: Bull. U.S. Nat. Mus., 79:26, 31 December 1912; Hatt, Jour. Mamm., 19:334, August 1938; Hershkovitz, Fieldiana-Zool., Chicago Nat. Hist. Mus., 31:552, 10 July 1951; Hatt, *et al.*, Cranbrook Inst. Sci. Bull., 33:59, March 1953; Hall and Kelson, The mammals of North America, 1:61, 31 March 1959; Alvarez and Martinez, Southwestern Nat., 12:205, 4 August 1967; Peterson, Jour. Mamm., 49:796, 26 November 1968.

Blarina mexicana, Gaumer, Monografía de los mamíferos de Yucatán, p. 249, 1917.

Cryptotis micrura, Murie, Misc. Publ. Mus. Zool., Univ. Michigan, 26:17, 15 July 1935 (part); Hall and Kelson, The mammals of North America, 1:63, 31 March 1959 (part).

Holotype.—Subadult female, skin (adult winter pelage) and skull, U.S. National Museum no. 108087, obtained on 5 February 1901 by E. W. Nelson and E. A. Goldman, original number 14495; type locality, Chichén Itzá, Yucatán.

Distribution.—Apparently limited to the Yucatan Peninsula except for an isolated population in the Balsas Basin of Guerrero (Fig. 15).

Measurements of holotype.—Total length 102; length of tail 29; length of hind foot 13; condylobasal length 18.8; palatal length 8.7; maxillary breadth 6.2; interorbital breadth 4.3; length of maxillary toothrow 7.4; cranial breadth 9.3; length of M2 1.3.

Color.—Dorsum in adult winter pelage “salt-and-pepper” grayish brown, near Olive-Brown or Hair Brown in specimens collected near the turn of the century; dorsum in adult summer pelage near Bister in specimen caught in 1929; dorsum in juvenal pelage speckled, bichromatic in appearance, near Chaetura Drab with

tips near Hair Brown in specimen obtained in 1910; venter in each pelage only slightly, if at all, paler than dorsum.

Comparisons.—From geographically adjacent populations to the south, *C. n. mayensis* differs in having significantly smaller external and cranial dimensions (Table 1), paler coloration, and more bulbous dentition. From *C. n. nigrescens*, *C. n. mayensis* differs in having notably paler pelage and more bulbous dentition.

Remarks.—*Cryptotis nigrescens mayensis* is one of the least well known taxa of the genus. Ten years elapsed between the original description of *mayensis* (Merriam, 1901:559), which was based on one specimen, and the capture of a second individual of the taxon. Soon thereafter, Gaumer (1917:249) recorded *mayensis* from 10 scattered localities in Yucatán. Subsequent records (Hatt, 1938:334; Hershkovitz, 1951:552; Hatt, *et al.*, 1953:59; Alvarez and Martinez, 1967:205; Peterson, 1968: 796) mostly have been based on individual specimens or fragmentary specimens from owl pellets or Mayan ruins.

Cryptotis nigrescens mayensis is the only shrew of the genus known to inhabit lowlands on the Yucatan Peninsula. Considerable local variation occurs among specimens from the peninsula, possibly because of the ubiquitous distribution of the species into habitats ranging from grassy roadside ditches to virgin quasi-rainforest. On the basis of morphological characters studied, however, there is no reason to doubt that gene flow generally is continuous among populations inhabiting various ecological situations, just as there is no reason to doubt intergradation with highland populations of the species to the south in Guatemala.

One aspect of the distribution of *mayensis* that defies explanation with specimens now available is the presence of a population apparently referable to that subspecies in the Balsas Basin of Guerrero. The sample available from that population consists of 24 partial crania that were removed from owl pellets found in a cave in the Cañon del Zopilote, 13 kilometers south of the bridge across the Río Mexcala near the village of Mexcala, at an elevation of about 2100 feet. That locality is separated from the nearest locality of record for *mayensis* on the Yucatan Peninsula by a distance of almost 600 miles, as well as by vast highland regions probably not suited for habitation by the species. Assignment of the owl pellet remains to *mayensis* necessarily is based solely on similarity of dental features and cranial and dental size, as the condition of preservation of the specimens precludes statistical analysis. Nevertheless, no differences whatsoever were detected by which the Guerreran shrews and those from the Yucatan Peninsula can be distinguished.

Three possible interpretations come to mind for unique distributions exhibited by *mayensis*. The first is that the population inhabiting the Balsas Basin does not represent *mayensis* at all, but rather is similar cranially and dentally as a result of parallel adaptations to analogous environmental conditions. Acquisition and study of complete specimens from Guerrero may reveal sufficient external or cranial differences to warrant description of the population inhabiting the Balsas Basin as a distinct subspecies. The second is that the subspecies is, or in Recent time was, represented by populations inhabiting low, arid regions ranging continuously from the Balsas Basin along valleys and plains across the mountains of Oaxaca, and finally to the Yucatan Peninsula. The third is that populations of the subspecies occur throughout the Balsas Basin, along the relatively arid Pacific coast of México southeast of the mouth of the Río Balsas, thence across the isthmus to the Gulf coastal plains, and finally to the Yucatan Peninsula. The lack of specimens from intervening areas cannot be used conclusively as an argument against any of the three alternatives because, as discussed above, specimens are difficult to collect and, consequently, poorly represented in museum collections. Moreover, specimens from owl pellets obtained in the Balsas Basin are from an area that has been sampled at one time or another by various field parties from numerous institutions, yet no specimens excepting those from owl pellets thus far have been obtained. This problem therefore remains an enigma pending acquisition and study of complete specimens from Guerrero or elsewhere in southern México.

Specimens examined.—237, as follows: YUCATÁN: 6 km. S Mérida, 1 (KU); Chichén Itzá, *ca.* 75 ft., 7 (1 AMNH, *5 UMMZ, USNM); Actun Spukil, *ca.* 200 ft., *149 (AMNH); *Uxmal*, *40 (INAH); Xbac, 1 (USNM); "Yucatán" (precise locality not specified), 1 (FMNH). QUINTANA ROO: 2 km. SE Laguna de Chichancanab, 1 (ENCB). CAMPECHE: La Tuxpeña, 1 (USNM). GUERRERO: Cueva del Cañón del Zopilate, 13 km. S Puente de Mexcala, *ca.* 2100 ft., *24 (UNAM). BRITISH HONDURAS: Baking Pot, 2 (1 BMNH, 1 ROM); "Central Farm" (not plotted), 1 (BMNH). GUATEMALA: Uaxactún, *9 (UMMZ).

Additional records (not plotted).—YUCATÁN: "Temax, Buctzotz, Calotmul, Senotillo, Valladolid, Nabalam, Izamal, Tzalam, Xbac" (Gaumer, 1917:249).

***Cryptotis nigrescens merriami*, new subspecies**

Holotype.—Adult female, skin (adult winter pelage) and skull, U.S. National Museum no. 77050, obtained on 21 December 1895 by E. W. Nelson and E. A. Goldman, original number 8846; type locality, Jacaltenango, 5400 ft., Huehuetenango, Guatemala.

Distribution.—Known from the Mesa Central of Chiapas as far west as Las Margaritas, throughout the highlands of Guatemala, Honduras, and El Salvador (Fig. 15), and probably also in north-central Nicaragua.

Measurements of holotype.—Total length 102; length of tail 33; length of hind foot 13.5; condylobasal length 19.6; palatal length 8.3; maxillary breadth 6.4; interorbital breadth 4.8; length of maxillary toothrow 6.7; cranial breadth 9.3; length of M2 1.5.

Diagnosis.—Size large for the species (Table 1); dorsum in adult winter pelage varying from Clove Brown to Bister or Sepia; dorsum in adult summer and juvenal pelages almost pure glossy black, darker than "Blackish Brown (3)"; venter in each pelage only slightly paler than dorsum although hairs tipped with gray or buff.

Comparisons.—From *C. n. mayensis*, *C. n. merriami* differs in being significantly larger, both externally and cranially (Table 1), in having darker coloration of pelage, and in having less bulbous dentition, especially as regards the unicuspids. From *C. n. nigrescens*, *C. n. merriami* differs in being significantly larger in every respect (Table 1), and in averaging paler in color of pelage.

Remarks.—Specimens herein referred to *merriami* have been reported previously as *Cryptotis nigrescens* by Goodwin (1942:117), Burt and Stirton (1961:21), and Hall and Kelson (1959:63). The geographic limits of the new subspecies are poorly defined because it is known from only 25 specimens. A specimen (not seen) from 2 mi. NW of Apaneca, Ahuachapán, El Salvador (Burt and Stirton, 1961:21) is referable to *merriami* on geographic grounds. Although samples are not yet sufficiently large to permit adequate analysis of intra-populational variation, the magnitude of differences in morphometric and pelage characteristics between *merriami* and adjacent populations justifies, in my opinion, subspecific recognition.

In terms of color, *merriami* merely represents a broad zone of intergradation between *nigrescens* and *mayensis*. Specimens from Guatemala (including the holotype of *merriami*) are almost intermediate in color between typical *nigrescens* and typical *mayensis* (possibly slightly nearer the latter), whereas the color of specimens of *merriami* from Honduras approaches that of typical *nigrescens*. In terms of size, however, intergradation is not so apparent and *merriami* seems to represent a cohesive genetic unit. Geographic variation in color apparently is clinal, with no distinct breaks, from one end of the distribution of the species to the other, but geographic variation in size involves two steps—from small on the Yucatan Peninsula to large in Chiapas, Guatemala, Honduras, and El Salvador, then to small again in Costa Rica and Panamá.

The name *merriami* is used in recognition of Dr. C. Hart Merriam, who, in addition to his many other contributions to mammalogy stemming largely from supervision of, and participation in, the activities of the Bureau of Biological Survey, was the first to

undertake description of variation in shrews now classified in the genus *Cryptotis*.

Specimens examined.—25, as follows: CHIAPAS: Volcán Kagchiná, ca. 4900 ft., °6 (JDS); *Cueva Los Llanos*, ca. 4900 ft., °3 (JDS). GUATEMALA: Jacaltenango, 5400 ft., 4 (USNM); La Primavera, 3200 ft., 7 (1 AMNH, °6 UMMZ). HONDURAS: San José, E of Llama, ca. 2400 ft., 1 (AMNH); Las Flores, 1 (AMNH); Montserrat Cloud Forest, near Yuscarán, 1 (MCZ). EL SALVADOR: Cerro Cacaquatique, 3500-4000 ft., 2 (UMMZ).

Cryptotis nigrescens nigrescens (J. A. Allen)

Blarina (Soriciscus) nigrescens J. A. Allen, Bull. Amer. Mus. Nat. Hist., 7:339, 8 November 1895.

Cryptotis *nigrescens*, Miller, Proc. Biol. Soc. Washington, 24:222, 31 October 1911.

Blarina micrura, J. A. Allen, Bull. Amer. Mus. Nat. Hist., 5:238, 22 September 1893.

Blarina nigrescens, Merriam, N. Amer. Fauna, 10:31, 31 December 1895.

Cryptotis merus Goldman, Smiths. Misc. Coll., 60(2):17, 20 September 1912, holotype from head of Río Limón, 4500 ft., Cerro Pirre, Darién, Panamá.

Cryptotis nigrescens, Goodwin, Bull. Amer. Mus. Nat. Hist., 87:288, 31 December 1946; Setzer, Jour. Washington Acad. Sci., 40:300, 15 September 1950; Hall and Kelson, The mammals of North America, 1:63, 31 March 1959 (part); Handley, Checklist of the mammals of Panama, in Ectoparasites of Panama, p. 756, 22 November 1966.

Cryptotis zeteki Setzer, Jour. Washington Acad. Sci., 40:299, 29 September 1950, holotype from Cerro Punta, 6500 ft., Chiriquí, Panamá; Hall and Kelson, The mammals of North America, 1:62, 31 March 1959.

Cryptotis tersus Goodwin, Amer. Mus. Novit., 1677:1, 28 June 1954, holotype from Santa Clara, 4200 ft., Chiriquí, Panamá; Hall and Kelson, The mammals of North America, 1:64, 31 March 1959.

Cryptotis mera, Hall and Kelson, The mammals of North America, 1:61, 31 March 1959.

Cryptotis nigrescens mera, Handley, Checklist of the mammals of Panama, in Ectoparasites of Panama, p. 756, 22 November 1966.

Cryptotis nigrescens zeteki, Handley, Checklist of the mammals of Panama, in Ectoparasites of Panama, p. 756, 22 November 1966.

Holotype.—Subadult, sex unknown, skin (adult winter pelage) and skull, American Museum of Natural History no. 9591/7952, obtained on 5 September 1891 by G. K. Cherrie, original number 2004; type locality, San Isidro, San José, Costa Rica.

Distribution.—Cloud forests on the cordilleras of Costa Rica and Panamá (Fig. 15).

Measurements of holotype.—Total length 87; length of tail 22; length of hind foot 12; condylobasal length 19.4; palatal length 8.2; maxillary breadth 6.5; interorbital breadth 4.6; length of maxillary toothrow 7.6; cranial breadth 9.4; length of M2 1.5.

Color.—Dorsum in adult winter pelage distinctly blackish or charcoal, but with faint brownish cast darker than Bister in specimen obtained in 1891, slightly

redder and darker than Clove Brown in specimen caught in 1953; specimens from Cerro Pirre, Panamá, that were collected in 1912 are slightly darker than those from Costa Rica, but retain the same charcoal cast; dorsum in adult summer pelage near Chaetura Black in a specimen taken in 1964; juvenal pelage indistinguishable from adult pelage except that it is slightly shorter and fuzzier and has less of a brownish cast; venter in each pelage only slightly paler, if at all, than dorsum.

Comparisons.—From *C. n. mayensis*, *C. n. nigrescens* differs most conspicuously in having darker pelage and less bulbous dentition. From *C. n. merriami*, *C. n. nigrescens* differs in having darker pelage and smaller external and cranial dimensions (Table 1).

Remarks.—All taxa of *Cryptotis* that have been described from Panamá (Goldman, 1912:17; Setzer, 1950:229; Goodwin, 1954b:1) excepting *C. endersi* Setzer are here considered as junior subjective synonyms of *C. n. nigrescens*. Handley (1966:756) recognized two subspecies of *C. nigrescens* in Panamá—*C. n. mera* Goldman from Cerro Pirre in eastern Panamá, and *C. n. zeteki* Setzer from Cerro Punta and Santa Clara in western Panamá—but noted: "These subspecies are poorly differentiated from typical *C. nigrescens* of Costa Rica." The differences in color between populations in eastern and western Panamá are slight, as are the differences between shrews from Panamá and those from Costa Rica, and are based on so few specimens that it is difficult to assess their significance. Statistical analyses revealed negligible variation in external and cranial dimensions among the known specimens from Costa Rica and Panamá, and I tentatively consider the variation in color as clinal within a single subspecies pending acquisition and study of adequate series taken in the same seasons. Although intergradation between populations of *nigrescens* inhabiting eastern and western Panamá presently is unlikely, the differences between the two populations are not nearly so marked as those that separate, say, *nigrescens* from *merriami*.

Two specimens (LACM 9859-60) of *nigrescens* lacking locality data but supposedly from Costa Rica, as well as the holotype of *C. n. nigrescens* (from San Isidro, Costa Rica) and one specimen (KU 84365) from 4½ kilometers northeast of Tilarán, Costa Rica, are as large cranially as the holotype and paratypes of *C. n. merriami*. Other specimens herein referred to the subspecies *nigrescens*, however, are substantially smaller cranially than specimens referred to *merriami*. At present, no logical explanation for this variation can be offered; there is no reason to believe that more than one species is present, and it seems likely that local, individual, or altitudinal variation is involved.

Specimens examined.—29, as follows: COSTA RICA: 4½ km. NE Tilarán, 1 (KU); 14 mi. N San Isidro de El General, 4800 ft., 1 (UMMZ); *San Isidro de El General*, 4700 ft., 1 (AMNH); *Volcán Irazú*, 9400 ft., 1 (AMNH); *Cerro Tablazo*, ca. 5000 ft., 1 (USNM); "Costa Rica" (precise locality not specified), 2 (LACM). PANAMÁ: *Cerro Punta*, 6500 ft., 2 (USNM); *Río Candela*, *Volcán de Chiriquí*, 6000 ft., 2 (AMNH); *Santa Clara*, 4200 ft., 11 (1 AMNH, 10 USNM); *Cerro Tacarcuna*, 4800 ft., 3 (USNM); *Cerro Malí*, 4700 ft., 1 (USNM); E slope *Cerro Pirre*, near head of *Río Limón*, 4500-5000 ft., 3 (USNM).

Relict Species

Three species (*C. gracilis*, *C. endersi*, and *C. magna*) are not closely related to any other Recent representatives of the genus *Cryptotis*, and are considered together as "relict species" on the basis of shared primitive characters. The group is one of convenience, probably is polyphyletic, and is employed pending acquisition of additional kinds of data to be used for analysis of interspecific relationships among the three species.

Cryptotis gracilis Miller

Cryptotis gracilis Miller, Proc. Biol. Soc. Washington, 24:221, 31 October 1911; Goodwin, Bull. Amer. Mus. Nat. Hist., 87:290, 31 December 1946; Hall and Kelson, The mammals of North America, 1:61, 31 March 1959.

Cryptotis orophila, Miller, Proc. Biol. Soc. Washington, 24:221, 31 October 1911.

Cryptotis jacksoni Goodwin, Amer. Mus. Novit., 1267:1, 10 December 1944, holotype from *Volcán Irazú*, Cartago, Costa Rica; Goodwin, Bull. Amer. Mus. Nat. Hist., 87:289, 31 December 1946; Hall and Kelson, The mammals of North America, 1:61, 31 March 1959.

Cryptotis orophila, Harris, Occas. Papers Mus. Zool., Univ. Michigan, 476:7, 8 October 1947.

Holotype.—Subadult, sex unknown, skin (adult winter pelage) and skull, U.S. National Museum no. 12236/38471, obtained on an unknown date by W. M. Gabb (catalogued 19 November 1874); type locality, head of *Río Larí*, near base of *Pico Blanco*, Limón (formerly Talamanca), Costa Rica.

Distribution.—Highlands of south-central Honduras and possibly adjacent Nicaragua; Cordillera Central and Cordillera de Talamanca of southeastern Costa Rica and western Panamá (Fig. 18); probably also on the Cordillera de Guanacaste in northwestern Costa Rica.

Measurements of holotype.—Condyllobasal length 18.6; palatal length 7.8; maxillary breadth 5.6; interorbital breadth 4.1; length of maxillary toothrow 6.9; cranial breadth 9.3; length of M2 1.3.

Diagnosis.—External characteristics: size medium for the genus (Table 1); tail elongate, averaging 52 per cent of length of head and body; front feet and claws small; all pelages distinctive; winter pelage only moderately luxuriant, with few vermiculations present; dorsum in juvenal pelage "salt-and-pepper" black (near Fuscous-Black), venter only slightly paler because of admixture of gray hairs with buffy tips; dorsum in summer and winter pelage "salt-and-

pepper" brown, varying from near Clove Brown to almost black in recently taken specimens (1961-67), venter only slightly paler; summer pelage differing from winter pelage only in being shorter and slightly less luxuriant.

Cranial characteristics: rostrum elongate, slender; braincase almost circular in dorsal outline; anterior limit of zygomatic plate above metastyle or between mesostyle and metastyle of M1; posterior limit of zygomatic plate at level of, or slightly posterior to, maxillary process, and above M3 or juncture of M2 and M3; dentition not bulbous; anterior element of ectoloph of M1 slightly reduced relative to posterior element; posterior surfaces of P4-M2 negligibly or only slightly recessed; protoconal basin of M1 slightly reduced relative to hypoconal basin; M3 consisting of paracrista, precentrocrista, postcentrocrista, vestigial metacrista, and well-developed metacone; talonid of m3 consisting of well-developed hypoconid and entoconid (specimen from Honduras lacks entoconid).

Comparisons.—Comparisons with *C. endersi*, *C. goldmani*, and *C. goodwini* are given in the accounts of those species.

From *C. nigrescens*, *C. gracilis* differs as follows: size larger in sympatric populations (Table 1); tail relatively and actually longer, averaging 52 (as opposed to 37-41) per cent of length of head and body; pelage usually longer, more luxuriant; rostrum relatively and actually more elongate; anterior element of ectoloph of M1 slightly reduced relative to posterior element (not reduced in *nigrescens*); protoconal basin of M1 slightly reduced relative to hypoconal basin; dentition not bulbous; well-developed metacone present on M3 (absent in *nigrescens*); talonid of m3 consisting of both hypoconid and entoconid (except in specimen from Honduras).

From *C. parva*, *C. gracilis* differs as follows: size larger, both externally and cranially (Table 1); tail relatively and actually much longer, averaging 52 (as opposed to 29-37) per cent of length of head and body; rostrum relatively and actually more elongate; braincase rounded in dorsal view, as opposed to almost pentagonal; posterior surfaces of P4-M2 less emarginate; well-developed metacone present on M3 (usually absent in *parva*); talonid of m3 consisting of both hypoconid and entoconid (except in specimen from Honduras).

From *C. mexicana*, *C. gracilis* differs as follows: tail relatively and actually longer, averaging 52 (as opposed to 33-42) per cent of length of head and body; rostrum relatively and actually longer and more slender; anterior element of ectoloph of M1 slightly reduced relative to posterior element; protoconal basin of M1 slightly reduced relative to hypoconal basin.

From *C. magna*, *C. gracilis* differs as follows: size markedly smaller, both externally and cranially (Table 1); rostrum relatively more elongate, much more slender; braincase less angular; protoconal basin of M1 slightly reduced relative to hypoconal basin; dentition not bulbous (moderately bulbous in *magna*); well-developed metacone present on M3 (metacone seldom present in *magna*).

Remarks.—*Cryptotis gracilis*, like *C. magna* and *C. endersi*, exhibits primitive characteristics of dentition and a long tail relative to length of head and body. These features probably indicate lack of substantial change from the ancestral condition. Another prominent anatomical feature of *gracilis* that is shared with *endersi* and to a lesser extent with *magna* is the elongate rostrum. The most obvious assumption would be that elongation of the rostrum is a form of

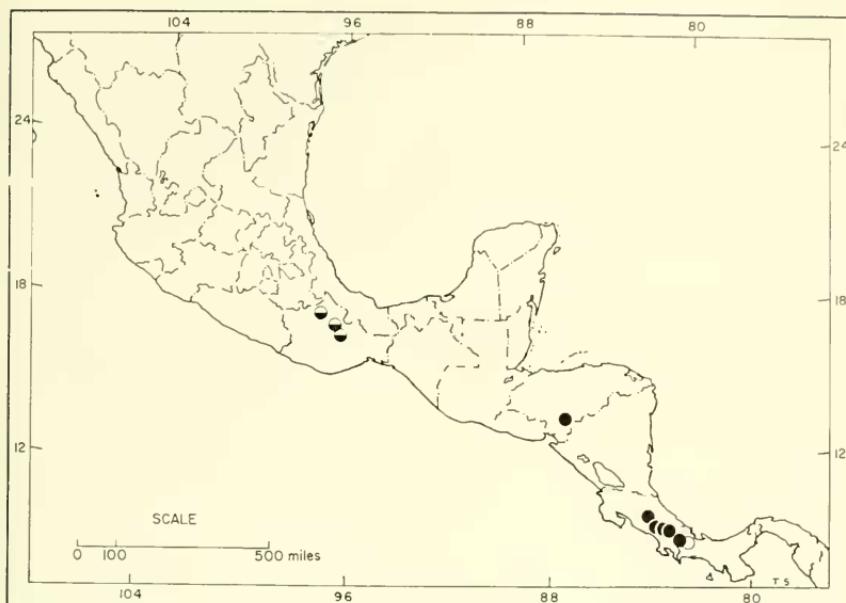


FIG. 18. Geographic distribution of *Cryptotis gracilis* (solid circles), *C. endersi* (open circle), and *C. magna* (circles solid below).

specialization, but if one considers that evolution in blarinine shrews apparently has involved reduction of dental formula and correspondent shortening of jaws to yield a more nearly optimal arrangement of fulcrum and lever, then the alternative interpretation seems more tenable. In any event, the rostrum in *gracilis* is conspicuously elongate, and the teeth are not at all crowded.

Goodwin (1944:1) described and named *Cryptotis jacksoni* on the basis of a single specimen from Volcán Irazú, Costa Rica. That same specimen (USNM 116649) previously had been assumed erroneously by Miller (1911:221) to be a topotype of *Cryptotis orophila* J. A. Allen for the purpose of comparison with three specimens of *C. gracilis*. The primary difference between *gracilis* and *jacksoni*, in which both Goodwin and Miller were in agreement (see also Goodwin, 1946:289), was that *jacksoni* had a broader skull. It now is apparent, however, that the breadth of the skull of the holotype of *jacksoni* falls within the normal variation of *gracilis*. A series of 10 specimens (LSU 12641-50) of *gracilis* from Cerro Asunción, Costa Rica, for example, includes specimens that are larger than the holotype of *jacksoni* as well as others that are almost as small as the holotype of *gracilis* (which is at the lower end of variation in size for Costa Rica). Furthermore, that same series encompasses the range of variation in color and other characteristics by which *jacksoni*

soni reputedly differed from *gracilis*. The name *jacksoni* thus must be relegated to the status of junior subjective synonym of *gracilis*.

One specimen (UMMZ 62885) from oak cloud forest at an elevation of 11,000 feet or a little higher on Cerro Las Vueltas, Costa Rica, originally was reported by Harris (1943:7) as *Cryptotis orophila* J. A. Allen. Goodwin (1946:290) correctly assigned that specimen to *gracilis*, but listed the elevation at the site of capture as 8000 feet.

With the exception of a single specimen (KU 106941) from Cerro Uyuca, Honduras, all the localities from which specimens of *gracilis* thus far have been obtained are on the Cordillera Central of Costa Rica or the Cordillera de Talamanca of Costa Rica and Panamá. The gap in distribution across Nicaragua may be of relatively Recent origin; on the other hand, it seems unlikely that habitat comparable to that inhabited by *gracilis* in Costa Rica ever has extended completely across Nicaragua (see also Duellman, 1966:718). Furthermore, the specimen from Honduras differs from typical Costa Rican individuals in being slightly smaller, both externally and cranially, and in having only one cusp (the hypoconid) as opposed to both hypoconid and entoconid on the talonid of m3. Acquisition and study of additional specimens from Honduras or the highlands of north-central Nicaragua may reveal a distinct subspecies of *C. gracilis*.

Data on reproduction are scanty, but seemingly demonstrate reproductive activity throughout much of the year. Young individuals in juvenal pelage have been collected in August and December; subadults in January, March, April, June, July, and August; adults in all months for which specimens are available; and old adults only in January. Two adult males from the Cerro Punta-Boquete trail, Panamá, one (USNM 322995) obtained on 9 February 1962 and the other (USNM 322996) on 14 March 1961, had enlarged testes, and two adult males (LSU 12643 and 12645) from Cerro Asunción, Costa Rica, had enlarged testes when caught on 19 January 1967. An adult female (USNM 322994) that was caught on the Cerro Punta-Boquete trail on 8 March 1962 contained a single embryo that measured 8 mm. in crown-rump length. An adult female (LSU 12650) from Cerro Asunción had a visibly swollen right uterine horn when captured on 6 April 1967. Another adult female (LSU 12657), which was obtained on 21 July 1967 on Cerro Chirripó, Costa Rica, contained four embryos.

Information on molt, like that on reproduction, is scarce. Specimens in winter pelage have been obtained in the months of January

through April, specimens molting from winter to summer pelage in January and March, and specimens in summer pelage in April, June, July, and August. Nothing is known of the time or duration of the autumnal molt.

Vegetation at the sites of capture of most of the specimens of *gracilis* presently available was oak cloud forest (generally at elevations ranging from 6500-9800 feet) or páramo (generally above 9800 feet). Costa Rican páramo is characterized by low mean temperature (5.4-7.5°C.), high relative humidity and annual precipitation (up to 2800 mm.), and shrub vegetation including abundant herbs and bamboo (Wagner, 1964:237). The specimen (KU 106941) from Cerro Uyuca, Honduras, was caught under a rotting log in pine forest.

Specimens examined.—42, as follows: HONDURAS: W slope of Cerro Uyuca, 12 km. WNW El Zamorano, ca. 5500 ft., 1 (KU). COSTA RICA: Hacienda El Retiro, Volcán Turrialba, ca. 8500 ft., 3 (UMMZ); 11 km. NNE Heredia, 1 (UMMZ); Volcán Irazú, ca. 10,400 ft., 2 (1 UMMZ, 1 USNM); Finca Coliblanca, ca. 7700 ft., 2 (UMMZ); Cerro Las Vueltas, 11,000-11,300 ft., 1 (UMMZ); N slope Cerro de la Muerte, ca. 10,940 ft., 3 (UMMZ); Cerro Asunción, ca. 11,000 ft., 10 (LSU); La Piedra, ca. 10,500 ft., 6 (LSU); head of Río Talari, Cerro Chirripó, ca. 11,600 ft., 8 (LSU); Cerro Estaquero, ca. 10,000 ft., 1 (LSU); head of Río Lari, near base of Pico Blanco, ca. 6000 ft., 1 (USNM). PANAMÁ: Cerro Punta-Boquete trail, 7600 ft., 3 (USNM).

Cryptotis endersi Setzer

Cryptotis endersi Setzer, Jour. Washington Acad. Sci., 40:300, 29 September 1950; Hall and Kelson, The mammals of North America, 1:60, 31 March 1959; Handley, Checklist of the mammals of Panama, in Ectoparasites of Panama, p. 756, 22 November 1966.

Holotype.—Young, sex unknown, skin (juvenile pelage) and skull, Academy of Natural Sciences of Philadelphia no. 20955, obtained on 24 July 1941 by R. K. Enders, original number 3310; type locality, Cylindro, above 4000 ft., Bocas del Toro, Panamá.

Distribution.—Known only from type locality (Fig. 18); probably occurs in isolated barrens on upper Caribbean slopes of the Cordillera de Talamanca in western Panamá and southeastern Costa Rica.

Measurements of holotype.—Total length 109; length of tail 36; length of hind foot 13; condylobasal length 20.4; palatal length 8.7; interorbital breadth 4.8; length of maxillary toothrow 7.5; cranial breadth 9.9; length of M2 1.6.

Diagnosis.—External characteristics: size medium for the genus (Table 1); tail elongate, 49 per cent of length of head and body; front feet and claws small; juvenile pelage practically indistinguishable from juvenile pelage in *C. n. nigrescens*; adult pelage unknown.

Cranial characteristics: rostrum exceptionally elongate, broad; braincase not angular; anterior limit of zygomatic plate above metastyle of M1; posterior limit of zygomatic plate above M3; dentition bulbous; anterior element of ectoloph of M1 not reduced relative to posterior element; posterior surfaces of P4-M2 not

recessed; protoconal basin of M1 not reduced relative to hypoconal basin; M3 consisting of paracrista, precentrocrista, vestigial postcentrocrista, and well-developed metacone; talonid of m3 consisting of hypoconid and entoconid, the latter not well developed.

Comparisons.—Comparisons with *C. magna*, *C. mexicana*, and *C. goodwini* are given in the accounts of those species.

From *C. nigrescens*, *C. endersi* differs as follows: size larger than in potentially sympatric populations (Table 1); tail relatively and actually longer, 49 (as opposed to 37-41) per cent of length of head and body; rostrum relatively and actually much more elongate; zygomatic plate situated slightly farther posteriorly; metacone present on M3 (never present in *nigrescens*); talomid of m3 consisting of both hypoconid and entoconid.

From *C. gracilis*, *C. endersi* differs as follows: rostrum relatively and actually more elongate; dentition bulbous; anterior element of ectoloph of M1 not reduced relative to posterior element.

From *C. parva*, *C. endersi* differs as follows: size larger than in potentially sympatric populations (Table 1); tail relatively and actually much longer, 49 (as opposed to 29-37) per cent of length of head and body; rostrum relatively and actually much more elongate; dentition bulbous; anterior element of ectoloph of M1 not reduced relative to posterior element; posterior surfaces of P4-M2 not recessed; protoconal basin of M1 not reduced relative to hypoconal basin; well-developed metacone present on M3 (absent in *parva*); talonid of m3 consisting of both hypoconid and entoconid.

From *C. goldmani*, *C. endersi* differs as follows: front feet and claws conspicuously smaller; tail relatively and actually longer, 49 (as opposed to 34-40) per cent of length of head and body; rostrum relatively and actually much longer; braincase less angular; dentition bulbous; anterior element of ectoloph of M1 not reduced relative to posterior element; posterior surfaces of P4-M2 not recessed; protoconal basin of M1 not reduced relative to hypoconal basin.

Remarks.—The holotype of *endersi* has a much longer rostrum relative to overall size of skull than any other nominal taxon of *Cryptotis*. Other external and cranial features, such as unreduced dentition and long tail relative to length of head and body, are shared with *C. gracilis* and *C. magna*. It is unlikely, however, that similarities among these taxa are indicative of close relationship; the three species probably represent an evolutionary grade rather than a clade.

Considerable thought has been given the possibility that the single specimen of *endersi* could be merely an extremely aberrant individual of *C. gracilis*. Such a situation is unknown, however, for any other species of *Cryptotis*. Furthermore, of the 35 specimens of *Cryptotis* presently available from Panamá, only the holotype of *endersi* was obtained on the northern slope of the cordilleras. As pointed out by Fairchild and Handley (1966:13) and Handley (1966:756), the site of capture (Cylindro, above 4000 ft.) of the holotype of *endersi* is on the northern slope of the Cordillera de

Talamanca, and therefore in Bocas del Toro Province rather than Chiriquí as originally reported (Setzer, 1950:300). The northern slope supports much more luxuriant vegetation than the southern slope because it receives substantially more rainfall (Vivó, 1964:213). Much of the area thus is covered with relatively undisturbed rainforest, and is characterized by almost inaccessible terrain and a paucity of human habitation. Within the rainforest, however, are isolated barrens with stunted trees and sparse ground cover. According to the collector, R. K. Enders, the holotype of *endersi* was caught in such a barren. Possibly the habitat is so poor in those places that *endersi* has survived as a result of reduced competition.

On the basis of its primitive dentition, elongate rostrum, and long tail relative to length of head and body, *endersi* is considered to be a relict that has had a long evolutionary history distinct from other Recent taxa, but which probably descended from the same precursor as did *C. gracilis*.

Specimen examined.—One, the holotype.

Cryptotis magna (Merriam)

Blarina magna Merriam, N. Amer. Fauna, 10:28, 31 December 1895.

Cryptotis magna, Miller, Bull. U.S. Nat. Mus., 79:28, 31 December 1912; Hall and Kelson, The mammals of North America, 1:62, 31 March 1959; Musser, Occas. Papers Mus. Zool., Univ. Michigan, 636:6, 17 June 1964; Jones and Genoways, Jour. Mamm., 48:321, 20 May 1967; Goodwin, Bull. Amer. Mus. Nat. Hist., 141:41, 30 April 1969.

Holotype.—Adult male, skin (adult summer pelage) and skull, U.S. National Museum no. 68575, obtained on 24 July 1894 by E. W. Nelson and E. A. Goldman, original number 6493; type locality, Totontepee, 6800 ft., Oaxaca.

Distribution.—Apparently restricted to the Sistema Montañoso in north-central Oaxaca (Fig. 18), but possibly also on the Sierra Madre del Sur in southern or western Oaxaca.

Measurements of holotype.—Total length 134; length of tail 42; length of hind foot 17; condylobasal length 23.7; palatal length 10.6; maxillary breadth 7.6; interorbital breadth 5.7; length of maxillary toothrow 9.0; cranial breadth 11.8; length of M2 1.9.

Diagnosis.—External characteristics: size largest of any species of the genus (Table 1); tail elongate, averaging 52 per cent of length of head and body; front feet relatively large, but claws strongly recurved and not especially large; juvenal pelage unknown; adult winter and summer pelages distinctive; winter pelage luxuriant, vermiculations numerous, dorsum varying from Mummy Brown to Bister in specimens collected in 1894, venter almost as dark, but slightly paler because of admixture of hairs with buffy tips, dorsum Clove Brown in specimens collected in 1959; summer pelage not particularly luxuriant, vermiculations sometimes present, dorsum "salt-and-pepper" black, varying from near Fuscous-

Black to Chaetura Black in recently taken specimens (1964), venter slightly paler.

Cranial characteristics: skull massive; rostrum elongate, broad; braincase angular; anterior limit of zygomatic plate above metastyle of M1; posterior limit of zygomatic plate at level of, or posterior to, maxillary process and above M3; dentition moderately bulbous; anterior element of ectoloph of M1 slightly reduced relative to posterior element; posterior surfaces of P4-M2 not recessed; protoconal basin of M1 not reduced relative to hypoconal basin; M3 consisting of paraerista, precentroerista, and postcentroerista; talonid of m3 consisting of both hypoconid and entoconid.

Comparisons.—Comparisons with *C. nigrescens*, *C. gracilis*, and *C. parva* are given in the accounts of those species.

From *C. goodwini*, *C. magna* differs as follows: size larger, both externally and cranially (Table 1); tail relatively and actually longer, averaging 52 (as opposed to 35) per cent of length of head and body; front feet about the same size, but claws not so large; posterior surfaces of P4-M2 not recessed; protoconal basin of M1 not reduced relative to hypoconal basin; dentition moderately bulbous (not bulbous in *goodwini*); M3 much less reduced, with precentroerista and postcentroerista usually present; talonid of m3 consisting of both hypoconid and entoconid.

From *C. goldmani*, *C. magna* differs in the same ways as from *C. goodwini* except as follows: difference in size even more pronounced (Table 1); talonid of m3 consisting of both hypoconid and well-developed entoconid, as opposed to usually consisting of hypoconid and vestigial entoconid in *goldmani* (in the region of sympatry).

From *C. mexicana*, *C. magna* differs as follows: size conspicuously larger (Table 1); tail relatively and actually longer, averaging 52 (as opposed to 33-42) per cent of length of head and body; rostrum relatively and actually more elongate; dentition moderately bulbous (not bulbous in *C. mexicana*).

From *C. endersi*, *C. magna* differs as follows: size conspicuously larger (Table 1); rostrum relatively less elongate; braincase much more angular.

Remarks.—*Cryptotis magna* was appropriately named, as it is substantially larger than other Recent representatives of the genus. The most conspicuous external feature of *magna* is its long tail, which averages approximately one-half as long as the combined length of head and body. The front feet in *magna* are large, but with claws that are more abruptly recurved and less highly developed and strongly supported than those of *goldmani* and *goodwini*. The massive skull and bulbous dentition are the most conspicuous cranial features.

Judging from all available data, *magna* is a relict, and is only remotely related to any other living species. The long tail and primitive cranial and dental characteristics (such as the relatively unreduced structure of the upper and lower third molars) would seem to indicate that *magna* is the only surviving representative of an ancient lineage. An interpretation of the evolutionary significance

of the apparent relationship of *magna* to the extinct *C. kansasensis* is provided beyond.

Cryptotis magna seemingly has a highly restricted distribution, but additional collecting may reveal that it occurs throughout suitable habitat on the Sistema Montañoso in Oaxaca. Elevations and habitats from which specimens presently available have been collected vary from 5200-9200 feet in cool, damp, pine-oak cloud forest with abundant philodendrons and tree ferns on the Sierra de Juárez (Musser, 1964:4, 6; Jones and Genoways, 1967:320-321), to 6800-8000 feet in dense, damp oak forest on Cerro Zempoaltepec and at Totontepec. The latter two localities are separated from the Sierra de Juárez by the rather abrupt drainage of the Río Cajonos, but specimens presently available do not exhibit demonstrable geographic variation.

Seven specimens (KU 99539-45), all from the vicinity of Vista Hermosa on the Sierra de Juárez, were caught in traps baited with tunafish that were set under logs or tree roots. An old adult male (KU 99544) had enlarged testes when caught on 25 June 1965.

Specimens examined.—11, all from OAXACA, as follows: San Isidro, ca. 8 mi. NE Comaltepec, ca. 7000 ft., 1 (AMNH); Vista Hermosa, ca. 5200 ft., 2 (KU); 3½ mi. SSW Vista Hermosa, 6200-7100 ft., 4 (KU); 12 mi. SSW Vista Hermosa, 9300 ft., 1 (KU); 12 mi. NE Llano de las Flores, 9200 ft., 1 (UMMZ); Totontepec, 6800 ft., 1 (USNM); Cerro Zempoaltepec, 8000 ft., 1 (USNM).

EXTINCT SPECIES OF *Cryptotis* AND *Paracryptotis*

Three extinct species of *Cryptotis* and two of a closely related genus, *Paracryptotis*, are known from Pliocene and early Pleistocene deposits in the western and central United States. One extinct species of *Cryptotis* and one of *Paracryptotis* have been referred in the past to the closely related genus *Blarina*. The relationships of the extinct species of *Cryptotis* and *Paracryptotis* have been assessed in order to provide a phylogenetic basis for classification of Recent Middle American species of *Cryptotis*.

Genus *Cryptotis* Pömel *Cryptotis adamsi* (Hibbard)

Blarina adamsi Hibbard, Jour. Paleont., 27:29, January 1953.

Cryptotis adamsi, Repenning, U.S. Geol. Surv. Prof. Paper, 565:39, 1967.

Holotype.—Left premaxillary and maxillary, including P2-M2, UMM 27267; from Univ. Michigan loc. UM-K1-47, Fox Canyon, sec. 35, T. 34 S, R. 30 W, XI Ranch, Meade Co., Kansas; late Pliocene (early Blancan), Rexroad formation, Rexroad fauna.

Diagnosis.—Dental formula, 1-5-1-3/1-2-3; dentition not bulbous; anterior limit of zygomatic plate slightly posterior to mesostyle of M1; posterior limit of

zygomatic plate slightly anterior to maxillary process; anterior element of ectoloph of M1 reduced relative to posterior element; posterior surfaces of P4-M2 slightly recessed; protoconal basin of M1 decidedly reduced relative to hypoconal basin; talonid of m3 slightly reduced and consisting only of hypoconid. Hibbard (1953:29-30) provided detailed descriptions of other features of the holotype and paratypes.

Comparisons.—Because *adamsi* originally (Hibbard, *op. cit.* :29) was described and named as a species of *Blarina* but later (Repenning, 1967:39) was transferred to *Cryptotis*, there is need for comparison with Recent taxa of both *Blarina* and *Cryptotis* as well as with extinct species of *Cryptotis* and *Paracryptotis*.

The configurations of M1 and M2 in *adamsi*, especially of their hypoconal basins, are similar to those in Recent *Blarina*. The upper unicuspids of *adamsi*, however, are not compressed antero-posteriorly as in *Blarina*, and the hypocone of P4 is not so highly developed. In labial view, the maxillary bone and dentition of *adamsi* resemble those of *Blarina* except that the anterior element of the ectoloph of M1 in the former is more highly reduced relative to the posterior element (in this respect approximating the condition in *C. parva*). The anterior border of the zygomatic plate is situated over the mesostyle of M1 as in certain taxa of both *Cryptotis* and *Blarina*, but the posterior border is above the mesostyle of M2 instead of farther posterior as in *Blarina*. The dentition of tropical and subtropical subspecies of *C. parva* closely resembles that of *adamsi* (U3-M1 of *adamsi* are almost identical with those of certain specimens of *C. parva orophila* and *C. p. tropicalis*), although in most Recent specimens the posterior surfaces of P4-M2 are more strongly emarginate. Likewise, the lower molars of *adamsi* are more like those of Recent tropical or subtropical *C. parva* than those of any Recent *Blarina*; the talonids of the lower molars in *adamsi* are not so highly developed as in *Blarina*.

Cryptotis adamsi differs from all other known taxa of *Cryptotis* (as well as *Paracryptotis*), extinct or Recent, in that U5 (which probably corresponds to P3) is retained. In other respects, the teeth of *adamsi* do not differ markedly from those of *C. meadensis*, except that specializations involving reduction of dentition characteristic of United States and northern Mexican populations of the *parva*-lineage are more pronounced in the latter. The teeth of *C. adamsi* exhibit none of the peculiar characteristics associated with development of robust dentition, and thus are readily distinguished from those of *Paracryptotis rex* and *P. gidleyi*.

Remarks.—Hibbard (1953:29) originally assigned *adamsi* to *Blarina* rather than *Cryptotis* because of the presence of five upper unicuspids and of other features of dentition he thought resembled *Blarina* more than *Cryptotis*. Repenning (1967:39-40) transferred *adamsi* to *Cryptotis*, stating that *adamsi* differs from species assigned to *Blarina* in ". . . (1) greater anteroposterior shortening of the talonid of m1, (2) more posterior placement of the metaconid of m1 relative to the position of the protoconid, (3) greater reduction of the heel of m3, (4) retention of a primitive blarinine mandibular

articulation and associated jaw structures, and (5) a rectangular M2."

Probably one reason for difficulty in establishing clear-cut criteria by which *adamsi* can be assigned to either *Cryptotis* or *Blarina* is that during the Hemphillian and earliest Blancan ages representatives of the genus *Cryptotis* were at a grade of evolution not far removed from *Blarina*. Most available evidence, in my opinion, supports classification of *adamsi* in the genus *Cryptotis*, but retention of five upper unicuspids probably indicates that *adamsi* stemmed from near the common ancestry of *Blarina* and *Cryptotis*.

Repenning (*op. cit.*:40) assigned a fragmentary specimen from the mid-Pliocene (Hemphillian) Christmas Valley local fauna of Lack County, Oregon, to *C. adamsi*. I have not seen that specimen, but would not be surprised if *adamsi* or its precursor occurred in western North America during the Hemphillian.

Specimens examined.—Holotype, paratypes, and additional material (UMMP) from the Rexroad fauna of Kansas.

Cryptotis meadensis Hibbard

Cryptotis? *meadensis* Hibbard, Jour. Paleont., 27:27, January 1953; Repenning, U.S. Geol. Surv. Prof. Paper, 565:40, 1967.

Holotype.—Posterior part of left ramus, including p4-m3, UMMP 27266; from Univ. Michigan loc. UM-K1-47, Fox Canyon, sec. 35, T. 34 S, R. 30 W, XI Ranch, Meade Co., Kansas; late Pliocene (early Blancan), Rexroad formation, Rexroad fauna.

Diagnosis.—Dental formula unknown; dentition not bulbous; talonid of m3 elongate, not especially reduced in length although apparently consisting only of hypoconid. Hibbard (1953:27-29) described the holotype (and only known specimen) of *meadensis* in detail, and compared it to Recent taxa of *Cryptotis*.

Remarks.—The holotype of *meadensis* is practically indistinguishable in size and morphological features from Recent specimens of *C. parva*, and probably was an early representative of the *parva*-lineage or the stem from which the *parva*-lineage diverged. The only conspicuously primitive dental characteristic that can be used to separate the holotype of *meadensis* from Recent specimens of *parva* is the talonid of m3; although consisting of only one cusp (the hypoconid), the talonid in *meadensis* is long relative to the trigonid (as opposed to shorter in *parva*). The possibility exists that *meadensis* had five upper unicuspids, but no upper dentitions have been found as yet.

Cryptotis meadensis apparently was contemporary with *C. adamsi* and *Paracryptotis rex*, and lived in Kansas at a time when

there probably existed ". . . a varied topography ranging from upland grassland areas to meadow flats and timbered areas at least along parts of the Upper Pliocene stream valleys. There is evidence that the climate in the Upper Pliocene was more equable than at present, without extremely cold winters or severely hot summers, and that there was a greater degree of humidity in the region than there is now" (Hibbard, 1950:177).

Specimen examined.—One, the holotype (UMMP).

Cryptotis kansasensis Hibbard

Cryptotis kansasensis Hibbard, Trans. Kansas Acad. Sci., 60:333, 1958; Repenning, U.S. Geol. Surv. Prof. Paper, 565:40, 1967.

Holotype.—Part of left maxillary including P4-M2, UMMP 34447; from Univ. Michigan loc. UM-K1-56, roadbank north of railroad along west edge of NW $\frac{1}{4}$ sec. 24, T. 30 S, R. 5 W, 1 $\frac{3}{4}$ mi. S, 1 mi. E Norwich, Kingman Co., Kansas; early Pleistocene, Meade group.

Diagnosis.—Dental formula, 1-4-1-3/1-2-3; dentition relatively bulbous; anterior limit of zygomatic plate approximately above metastyle of M1; posterior limit of zygomatic plate above M3; anterior element of ectoloph of M1 reduced relative to posterior element; posterior surfaces of P4-M2 not recessed; M3 consisting of at least paracrista and precentrocrista, and possibly also postcentrocrista; protoconal basin of M1 almost equal in size and development to hypoconal basin; talonid of m3 consisting of only one cusp, the hypoconid. Hibbard (1958:333-334) provided detailed descriptions of other features of the holotype and paratype.

Comparisons.—As was surmised by Repenning (1967:40), the upper and lower dentitions and the mandible of *C. kansasensis* are similar to those of the Recent *C. magna*. Noteworthy differences between available specimens of *kansasensis* and *magna* are: M2 in *kansasensis* is relatively much narrower antero-posteriorly, and the hypoconal basin is expanded much less; the crowns of all teeth are considerably higher in *kansasensis*; the infraorbital foramen, although situated in about the same position, is much more deeply excavated in *kansasensis*; the talonid of m3 in *kansasensis* has only one cusp (as opposed to two in *magna*).

Remarks.—The bulbous dentition and close resemblance in size and structure with *C. magna* would seem to indicate that *kansasensis* was a Blancan representative of a stem leading to the Recent *C. magna*. Because of the reduced structure of m3 and of other specializations, however, it is doubtful that *kansasensis* was the precursor of *magna* or any other nominal taxon.

Specimens examined.—Holotype and paratype (UMMP) from the early Pleistocene of Kansas.

Genus *Paracryptotis* Hibbard
Paracryptotis rex Hibbard

Paracryptotis rex Hibbard, Contrib. Mus. Paleont., Univ. Michigan, 8:122, 29
June 1950; Repenning, U.S. Geol. Surv. Prof. Paper, 565:41, 1967.

Holotype.—Anterior part of skull with complete dentition, and part of left ramus including m1-m3, UMMP 25172; from Univ. Michigan loc. UM-K1-47, Fox Canyon, XI Ranch, Meade Co., Kansas; late Pliocene (early Blancan), Rexroad formation, Rexroad fauna.

Diagnosis.—Dental formula, 1-4-1-3/1-2-3; dentition decidedly bulbous; anterior limit of zygomatic plate above parastyle of M1; posterior limit of zygomatic plate above mesostyle of M2; anterior element of ectoloph of M1 reduced relative to posterior element; posterior surfaces of P4-M2 not at all or only slightly recessed; protoconal basin of M1 not reduced relative to hypoconal basin; talonid of m3 consisting of well-developed crescentic-shaped hypoconid and possibly an entoconid. Hibbard (1950:121-127) provided detailed descriptions of other features of the holotype and paratypes.

Comparisons.—The dentition of *P. rex* is more robust than that of *Blarina* or of the most bulbous-toothed representatives of the genus *Cryptotis*. The upper dentition of *P. rex* superficially resembles that of *B. brevicauda* except as follows: P4 trapezoidal in outline rather than rectangular; posterior end of M2 rotated farther lingually; protoconal basin of M3 much less highly developed; unicuspids not compressed antero-posteriorly as in *Blarina* (rather, unicuspids structurally similar to those of *C. nigrescens mayensis*); crowns of teeth almost twice as high as in *B. brevicauda*; second upper unicuspid, unlike that of *Blarina*, slightly caniniform, and fourth displaced lingually so that it cannot be seen in labial view in most specimens; anterior element of ectoloph of M1, in contrast to *Blarina*, not especially reduced relative to posterior element; infraorbital foramen much more deeply excavated than in *Blarina*. Additionally, none of the specimens of *P. rex* examined have incompletely fused anterior and posterior contributions to the mesostyles of M1 and M2, as is common in *Blarina*.

The only Recent species of *Cryptotis* that even approaches *P. rex* in size, proportions, and other features is *C. magna*. The teeth in *C. magna* are almost as robust relative to overall size as in *P. rex*, but there is much less cingular development and greater expansion of the hypoconal basin in *C. magna* than in *P. rex*. The labial configuration of M1 in *P. rex* is more like that of *C. magna* than of *Blarina*. The metaconids of the lower molars of *P. rex* are situated posterior relative to the protoconids, as in *Cryptotis*, but the talonid of m3 apparently is unreduced and *Blarina*-like. More extensive comparisons of *P. rex* with representatives of other genera and with *P. gidleyi* are provided by Hibbard (1950:122-127) and Hibbard and Bjork (1970).

Remarks.—*Paracryptotis rex* is one of the most distinctive representatives of the tribe Blarinini. Recognition at the generic level is justified by strict adherence to the "degree of difference" definition necessarily followed by most paleontologists; *P. rex* differs as much dentally and cranially from *Blarina* and *Cryptotis* as either of these genera differs from the other. *Paracryptotis rex* has more characters

in common with *Cryptotis* than with *Blarina*, and probably resulted from radiation of the blarinine stem at some time after divergence of *Blarina*. This information, together with the fact that *P. rex* and *P. gidleyi* differ almost as much from one another as either does from *Cryptotis*, could be used as the basis for tentative consideration of *Paracryptotis* merely as a subgenus of the genus *Cryptotis*. Conversely, a separate genus or subgenus could be erected for *gidleyi*. It seems to me, however, that the current level of understanding of late Tertiary shrews is insufficient to warrant more than descriptive analysis, and that sweeping changes in classification should await accumulation and study of additional material.

Paracryptotis rex is known from the mid-Pliocene (Hemphillian) Rome fauna of Oregon, as well as from the late Pliocene (early Blancan) Rexroad fauna of Kansas. If the single specimen (not seen) from the Rome fauna that was assigned by Repenning (1967: 41) to *P. rex* indeed is a *Paracryptotis*, then it may represent a distinct morphological species that was the precursor of *P. rex*.

Specimens examined.—Holotype, paratypes, and other material (UMMP) from the Rexroad fauna of Kansas.

Paracryptotis gidleyi (Gazin)

Blarina gidleyi Gazin, Jour. Mamm., 14:142, May 1933; Repenning, U.S. Geol. Surv. Prof. Paper, 565:43, 1967.

Paracryptotis gidleyi, Hibbard and Bjork, Contrib. Mus. Paleont., Univ. Michigan (in press).

Holotype.—Fragmentary left ramus, including m1-m3, USNM 12650; from T. 7 S, R. 13 E, near Hagerman, Idaho; Hagerman lake beds, late Pliocene (early Blancan).

Diagnosis.—Dental formula, 1-4-1-3/1-2-3; dentition bulbous; anterior limit of zygomatic plate approximately above parastyle of M1; posterior limit of zygomatic plate between mesostyle and metastyle of M2; posterior surfaces of P4-M2 decidedly recessed; protoconal basin of M1 reduced relative to hypoconal basin; talonid of m3 consisting of both hypoconid and entoconid. Gazin (1933:142-144) described additional features of the holotype, and Hibbard and Bjork (1970) have studied material subsequently collected.

Comparisons.—Comparisons with other genera, as well as reasons for assigning *gidleyi* to *Paracryptotis*, were given by Hibbard and Bjork (*op. cit.*). Excepting minor structural differences in the coronoid process, the mandible of *gidleyi* matches that of *Cryptotis magna*. The positioning of the metaconids on molars of *gidleyi* is the same as in *Cryptotis*; they are situated farther posterior relative to the protoconids than in *Blarina*. The upper molariform teeth resemble those of *C. parva* in degree of posterior emargination and development of hypoconal basin. As in *C. adamsi* and *P. rex*, the maxillary process is situated well anterior to the mesastyle of M2. The infraorbital foramen is located above the parastyle of M1 and extends anterior as far as the metacone of P4, where it

forms a noticeable indentation in the maxillary; the posterior border is situated between the mesostyle and metastyle of M2 about as in *C. parva*.

Remarks.—Almost as many reasons could be given for assigning *gidleyi* to *Cryptotis* as have been listed by Hibbard and Bjork (*op. cit.*) for assignment to *Paracryptotis*. Judging from its specialized dentition, *gidleyi* did not give rise to any other nominal taxa and may represent a lineage derived from near the origin of *Paracryptotis* from the blarinine stem. *Paracryptotis gidleyi* is known only from the late Pliocene (early Blancan) Hagerman fauna of Idaho.

Specimens examined.—Approximately 20 specimens (UMMP) from the Hagerman fauna of Idaho.

PHYLOGENY AND ZOOGEOGRAPHY Phylogenetic Patterns

In his review of the Soricidae, Repenning (1967) recognized five subfamilies: the Heterosoricinae, Limnoecinae, and Allosoricinae (including only extinct genera known from the middle to late Tertiary), and the Crocidurinae and Soricinae (including both extinct and extant genera). The Soricinae was subdivided further into three tribes: the Blarinini, Soricini, and Neomyini. Available paleontological evidence suggests that of the three only the Blarinini is autochthonous to the New World; the earliest known representative of the Blarinini, *Adeloblarina berklandi* Repenning from the late Miocene (late Barstovian?) of Oregon, reputedly was not far removed from the basic stock of the Soricinae (Repennning, *op. cit.*:62).

The geological time period during which divergence of *Blarina* and *Cryptotis* occurred thus far has not been documented. The transfer of *Blarina adamsi* Hibbard to *Cryptotis* by Repenning (*op. cit.*:39) and of *B. gidleyi* Gazin to *Paracryptotis* by Hibbard and Bjork (1970) effectively eliminated the fossil record of *Blarina* prior to the Pleistocene, but certain characteristics of Pleistocene and Recent representatives of *Blarina*, such as retention of P3 and antero-posterior compression of unicuspids, suggest that divergence probably occurred prior to the time of deposition of the Rexroad and Hagerman faunas in the Pliocene.

One factor that may have been involved in divergence of *Cryptotis* and *Blarina* was resolution of a functional problem associated with feeding. The long rostra and jaws characteristic of shrews are not especially well adapted for mastication of hard foods because of the posterior placement of the fulcrum (jaw articulation). Functional problems associated with utilization of a variety of hard foods presumably were greater in early blarinine shrews than in their

living counterparts because of the primitive, distal placement of the articulation and relatively unspecialized features of the jaws and skull. Modifications of the primitive morphological scheme that undoubtedly have contributed to more efficient utilization of foods include: fusion of cranial sutures and replacement of cancellous bone with compact bone to provide a more nearly rigid ingestive apparatus; elimination of zygomatic arches, posterior relocation of maxillary processes and associated musculature, reduction and modification of the masseteric musculature, and development of paired articular facets and an internal temporal fossa on the dentary, all of which interact to permit increased speed and force in mastication; separation of the paired articular facets and concomitant anterior displacement of the ventral facet to provide more nearly optimal placement of the fulcrum; and shortening of the rostrum and jaws to decrease the length of the lever (in part from Gaughran, 1954).

Selection for decrease in length of jaws seemingly was correlated with selection for decrease in length of upper and lower toothrows. So far as the upper toothrows of shrews of the tribe Blarinini are concerned, shortening of functional masticatory surfaces has been facilitated principally in one or the other of two ways: antero-posterior compression of three of the five unicuspids (as in *Blarina*); or reduction in number of unicuspids (as in *Cryptotis* and *Paracryptotis*). Both adaptations evidently have proved successful, but in Recent *Blarina* there is also a tendency for reduction of number of unicuspids (see Choate, 1968). It should be noted that Recent shrews of the genus *Blarina* possess venomous salivary glands (Pearson, 1942 and 1950), but studies on other genera, including *Cryptotis*, thus far have not been sufficient to permit interpretation of the possible relationship of this adaptation to feeding or phylogeny.

Judging from the close relationship of *Cryptotis* to *Paracryptotis*, divergence of *Paracryptotis* probably took place after divergence of *Blarina*. *Paracryptotis* may have been the first, and most extreme, of several parallel experiments in development of bulbous teeth. Information as to the adaptive significance of bulbous teeth is not sufficient to permit speculation on the recurrent parallel evolution of this peculiar characteristic in several different lineages.

The known genera of the Blarinini, therefore, probably were established by late in the Tertiary, and divergence of lineages antecedent to living taxa accordingly occurred early. All known Pleistocene and Recent species of the genus *Cryptotis* can be classified as representatives of one or another of four such lineages: the *parv-* group, *mexicana*-group, *thomasi*-group, and a group of Middle

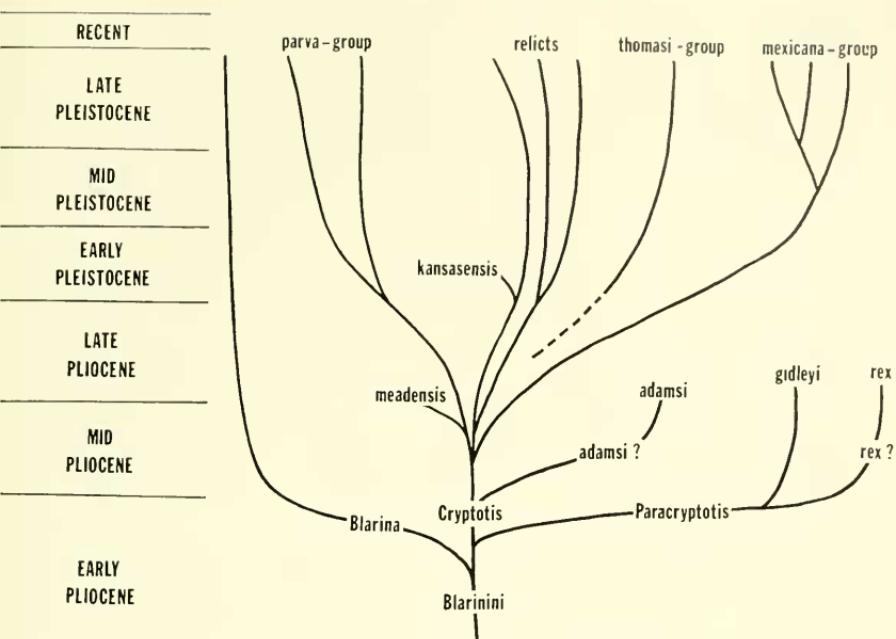


FIG. 19. Possible phylogenetic relationships of the genera *Cryptotis*, *Paracryptotis*, and *Blarina*, of extinct species of those genera, and of species-groups of the genus *Cryptotis*.

American relicts. I realize that species-groups have no formal taxonomic significance, but prefer use of those categories as a convenient method of emphasizing relationships without necessitating proposal of additional nomenclatorial categories, such as subgenera.

Centers of Origin and Dispersal

The earliest records of blarinine shrews are from the northwestern United States. By late in the Pliocene, radiation of several taxa of *Cryptotis* and *Paracryptotis* had taken place (Fig. 19), and by that time at least four species were present on the southern Great Plains. Recent zoogeographic patterns indicate that most subsequent radiation in *Cryptotis* occurred in southern México.

In the absence of an adequate fossil record for Middle American mammals, the hypothesis that southern México was the center of origin and dispersal of most Recent taxa of *Cryptotis* necessarily is based on the following observations: (1) the greatest number of species are represented in southern México; (2) the most highly specialized species occur there; and (3) subspecies are better differentiated there than in other parts of the range (criteria modified from Hooper, 1952:200). Of the three Recent species (*mexicana*,

goldmani, and *parva*) of *Cryptotis* with extensive distributions in México, only *mexicana* conforms to a fourth frequently quoted criterion—it is represented by greater specialization in the geographic area (southern México) suggested to have been its center of origin than in other parts of its range. In both *goldmani* and *parva*, on the other hand, the most highly specialized dental and cranial characteristics are found in populations located farther to the north, on the Cordillera Volcánica and in the United States, respectively. The one Middle American species (*nigrescens*) with an extensive distribution in Central America exhibits much greater specialization in southernmost México than farther to the south.

Further analysis of zoogeographic relationships shows that all of the Recent species of *Cryptotis* belong to one or the other of two geographic assemblages: those species (*magna*, *mexicana*, *goldmani*, and *parva*) that underwent radiation and dispersal primarily west of the Isthmus of Tehuantepec; and those species (*gracilis*, *endersi*, *goodwini*, *nigrescens*, and the *thomasi*-group) that underwent radiation and dispersal primarily east of the isthmus. Every representative of the former assemblage except *magna* secondarily has invaded niches east of the isthmus, whereas of the latter category only *nigrescens* has become established secondarily west of the isthmus. One or more species ancestral to the *thomasi*-group successfully emigrated to South America, where diversity of habitats on the Andes and apparent lack of substantial competition permitted rapid radiation of phenetically distinct taxa.

The two geographic associations do not correspond to the species-groups previously listed; rather, the associations subdivide the groups, and thereby provide clues concerning factors that probably influenced divergence of the species that comprise them. Within the *parva*-group, one species (*parva*) owes the majority of its diversity to radiation west of the isthmus, whereas the other species (*nigrescens*) undoubtedly underwent most of its evolution east of the isthmus. Within the *mexicana*-group, two species (*mexicana* and *goldmani*) are considered western in origin, whereas the third (*goodwini*) apparently evolved east of the isthmus. Of the so-called relicts, *magna* probably is autochthonous to cloud forests west of the isthmus, whereas *gracilis* and *endersi* are strictly eastern in origin. These facts lead to the premise that the Isthmus of Tehuantepec has had an influential effect on the diversity and interrelationships of Recent species of *Cryptotis*.

Of the four species-groups recognized herein, two (the *parva*-group and the group of relicts) are too poorly known ecologically

and phylogenetically to justify more than a few comments regarding interrelationships of the included species. The affinities of the taxa that comprise the *thomasi*-group will be discussed in a forthcoming review of the systematics of that group. The *mexicana*-group will be discussed in considerable detail in a separate section beyond.

The three Recent species (*endersi*, *gracilis*, and *magna*) of *Cryptotis* that are termed herein as "relicts" may not represent a hierarchical group. They are classified together solely on the basis of shared primitive characteristics, including elongate tail and rostrum and primitive dental configurations. Two (*endersi* and *gracilis*) of the three species evidently originated in Central America, possibly from a common ancestor, whereas the third (*magna*) has northern affinities. It is noteworthy in this respect that *C. kansasensis*, from the early Pleistocene of Kansas, apparently was related to *magna*, but was more advanced dentally. This serves to emphasize the appropriateness of the term "relict species."

The geographic and ecologic distributions of the three relict species are highly restricted. *Cryptotis magna* apparently is autochthonous to cool, damp, virgin cloud forests on the Sistema Montañoso in Oaxaca. *Cryptotis endersi* is known only from a soggy barren with stunted trees and sparse ground cover on the upper northern slope of the Cordillera de Talamanca in Panamá. *Cryptotis gracilis* occurs primarily in páramo vegetation in Costa Rica and Panamá, but also inhabits oak cloud forests at lower elevations, and is known from pine cloud forest in Honduras. *C. gracilis* is the least specialized dentally of the three and exhibits no tendency for development of characters associated with bulbosity. Restriction of suitable habitat associated with climatic changes at the termination of glaciation apparently resulted in isolation of a population of *gracilis* in Honduras, but permitted secondary utilization of páramo vegetation in Costa Rica and western Panamá.

The two Recent species (*parva* and *nigrescens*) and one extinct species (*meadensis*) of the *parva*-group are characterized by reduced dental configurations relative to those of most other extant species. This may indicate that divergence of the *parva*-group from other lineages preceded the origin of *meadensis*, and thus occurred as early as late or middle Pliocene (Fig. 19). Dental features reminiscent of those of the *parva*-group were well established in *C. adamsi* by the late Pliocene, even though *adamsi* was not far removed morphologically from the divergence of *Blarina* and *Cryptotis* and probably represented a distinct, terminal lineage. Dental features of *C. meadensis*, from the late Pliocene, are almost indistinguishable

from those of Recent *parva*, this possibly indicating that adaptations and specializations peculiar to *parva* already were at an advanced stage of development.

The ancestral species of the *parva*-group probably occurred in mesic grasslands of central and southern regions of the United States and México. *Cryptotis parva* is known from various Pleistocene faunas in the United States, but none provides clues concerning divergence of *parva* and *nigrescens* because radiation of those species probably already had occurred in southern México. The Isthmus of Tehuantepec seemingly was involved in at least some remote way in divergence of the two species; possibly *nigrescens* or its precursor emigrated across the isthmus and eventually became established in montane habitats, whereas *parva* remained west of the isthmus in grassland habitats. Adaptations by *nigrescens* for lowland habitats probably are secondary, as are adaptations by *parva* for montane habitats. The two species presently are at least partially sympatric throughout much of Central America, and occasionally are taken together in the same trapline.

Radiation of the *mexicana*-group

The fossil record provides no clues as to the time or place of origin of the *mexicana*-group (Fig. 19), but it is assumed that the group originated in southern México where little is known of Pleistocene or pre-Pleistocene mammalian micro-faunas. The only known fossils that pertain to the *mexicana*-group are 22 rami tentatively referred to *C. mexicana obscura* from a late Pleistocene (probably interglacial) deposit in San Josecito Cave, near Aramberri, Nuevo León (Findley, 1953). Perusal of zoogeographic patterns of the three Recent species (*mexicana*, *goldmani*, and *goodwini*), however, has shown that divergence can be explained in terms of modifications of distributional patterns resulting from a fluctuating climate.

Cryptotis mexicana occurs primarily in humid pine-oak forests and in cloud forests on the Sierra Madre Oriental, on both the Sistema Montañoso and Sierra Madre del Sur in Oaxaca, and on the Mesa Central in Chiapas (Fig. 6). *Cryptotis goldmani* occurs primarily in fir forests in which there is abundant sacatón grass, and at lower elevations extends into cloud forests, on the Cordillera Volcánica, the Sierra Madre del Sur, the Sistema Montañoso, across the Isthmus of Tehuantepec onto the Mesa Central, and on the highlands of western Guatemala (Fig. 9). *Cryptotis goodwini* apparently is restricted primarily to virgin pine-oak forests and cloud forests on the highlands of Guatemala and El Salvador (Fig. 6). *C. goodwini*

and *C. goldmani* are potentially sympatric, although they have never been taken together, in Guatemala; *C. goldmani* and *C. mexicana* are geographically sympatric throughout much of Oaxaca and occasionally are obtained at the same locality, although more frequently only one or the other species is caught in a given ecological situation.

Of the three species, *mexicana* is by far the most primitive, exhibiting few specializations of dentition and no obvious adaptations for a semi-fossorial mode of existence. Furthermore, *mexicana* apparently is the most ubiquitous of the three as regards habitat preference. *Cryptotis goodwini* is the most highly specialized of the three, having reduced dental configurations and pronounced external morphological adaptations to facilitate semi-fossorial habits. Accordingly, *goodwini* apparently has more restricted habitat preferences than either of the other species. *Cryptotis goldmani* is less specialized dentally than *goodwini*, but is equally as specialized with respect to external adaptations for a semi-fossorial mode of existence.

In Oaxaca, where *goldmani* and *mexicana* are sympatric, *mexicana* is represented by two subspecies. One of those (*C. m. mexicana*, on the Sistema Montañoso) is easily distinguished from *goldmani* by its relatively small size and unspecialized dental characteristics. The other subspecies (*C. m. peregrina*, on the Sierra Madre del Sur), however, is larger and exhibits external, cranial, and dental features that approach what might be expected of a population intergrading with *goldmani*. Likewise, Oaxacan populations of *goldmani* are less specialized with respect to dentition than those in other parts of the range of the species, and tend to resemble Oaxacan populations of *mexicana*. Wherever the two species have been collected in close proximity in the same ecological situation, however, specimens can be assigned to one or the other species with relative ease. In fact, noticeable character displacement occurs, and the two species can be distinguished readily on the basis of external features: specimens of *mexicana* have dark gray (almost black) dorsal pelage, whereas those of *goldmani* have relatively pale, distinctly brownish gray dorsal pelage; the ventral pelage of *mexicana* is only slightly paler than the dorsal pelage, whereas the ventral pelage of *goldmani* is pale drab brown (almost white in bright light); the front feet and claws of *mexicana* are less than half as large as those of *goldmani*, and tend to be black as opposed to unpigmented in *goldmani*. Displacement of cranial and dental characters is not so pronounced, but it is less difficult to separate crania of the two species where they occur together than from places where the two are separated ecologically.

Ecological separation apparently is related to habitat and elevation; in the vicinity of San Miguel Suchixtepec, specimens of *mexicana* have been examined from localities on the southern slope of the Sierra Madre del Sur at elevations ranging from 4275 to almost 7500 feet, whereas specimens of *goldmani* were taken there at elevations ranging from about 7400 to more than 9000 feet. In certain situations, however, the preferred habitats interdigitate in some impereceptible manner. For example, 24 specimens of *mexicana* and five specimens of *goldmani* have been examined from similar habitats at elevations ranging from 8000 to 10,500 feet on Cerro Zempoaltepec.

Perusal of the interrelationships of *mexicana* and *goldmani* in their region of sympatry has led me to consider those species as relatively recently divergent siblings, and has permitted formulation of a simple hypothesis pertaining to past events that may have influenced the present zoogeographic patterns of the representatives of the *mexicana*-group.

Evidence accumulated in this study indicates that the highlands of Oaxaca represent the center of radiation of the Recent species of the *mexicana*-group. At some time in the past a single species differing little, if at all, from Recent *mexicana* probably occurred throughout the forested highlands of southern and eastern México and Guatemala (Fig. 20A). An increase in aridity beyond that which exists today on the Isthmus of Tehuantepec would have isolated the precursor of *goodwini* on the mountains of Chiapas and Guatemala, thereby restricting *mexicana* or its precursor to mesic regions on the mountains of southern México (Fig. 20B). Further increase in aridity would have eliminated gene flow across the already relatively arid highlands of central Oaxaca, effecting isolation of the precursor of *goldmani* on the Sierra Madre del Sur and restricting *mexicana* to the Sierra Madre Oriental and the Sistema Montañoso (Fig. 20C). Because of differences in vegetation and topography, the break in gene flow across central Oaxaca probably would not have been so complete as that across the isthmus, with the result that fluctuations in climate such as those that occurred during the Pleistocene could have permitted intermittent genetic exchange between the two incipient species, *mexicana* and *goldmani*, but probably did not permit gene flow with the isolated *goodwini*. This would account for lack of gross morphological divergence between *mexicana* and *goldmani* as compared with that between either of those species and *goodwini*. During periods of partial sympatry of *mexicana* and *goldmani*, and possibly even at the present time, occasional hybridization with

selection against resulting hybrids hypothetically would reinforce the observed character displacement, which seemingly represents a primary isolating mechanism in the absence of ecological separation. Whatever the case, the three Recent species of the *mexicana*-group apparently underwent sufficient ecological specialization, and morphological divergence associated with that specialization, that they behave as biological species now that sympatry again has been achieved (Fig. 20D).

SUMMARY

A systematic review of Middle American representatives of the genus *Cryptotis*, based on examination of about 2200 specimens representing 34 nominal taxa, revealed eight recognizable species in that region. Biometrical analyses of intra- and inter-populational variation demonstrated that four of those species (*gracilis*, *endersi*, *magna*, and *goodwini*) exhibit no appreciable geographic variation and are monotypic, whereas the other four (*mexicana*, *goldmani*, *parva*, and *nigrescens*) are polytypic. Clinal geographic variation was described, but was not recognized nomenclaturally except when pronounced breaks in clines corresponded geographically or ecologically to apparent breaks in gene flow among populations.

The first of the four polytypic species, *C. mexicana*, was interpreted to consist of four well-differentiated subspecies: *C. m. obscura*, which occurs primarily in upper humid tropical forests at middle elevations on the Sierra Madre Oriental from southern Tamaulipas to northern Puebla; *C. m. mexicana*, which occurs primarily in cloud forests at middle elevations on the Sierra Madre Oriental, Sistema Montañoso, and across the Isthmus of Tehuantepec on the Mesa Central of Chiapas; *C. m. nelsoni*, which is known only from upper humid tropical forest at middle elevations on Volcán San Martín in southern Veracruz; and *C. m. peregrina*, which occurs primarily in cloud forests on the Sierra Madre del Sur in Oaxaca.

Cryptotis goldmani was interpreted to consist of two subspecies, *C. g. alticola*, which occurs at high elevations in fir forests on the Cordillera Volcánica, and *C. g. goldmani*, which occurs in similar habitats, but also ranges down into cloud forests, on the Sierra Madre del Sur, Sistema Montañoso, across the Isthmus of Tehuantepec onto the Mesa Central of Chiapas, and on the highlands of western Guatemala.

Middle American populations of *C. parva* were interpreted as pertaining to one or another of five distinctive subspecies: *C. p. berlandieri*, which occurs at low or middle elevations in mesic

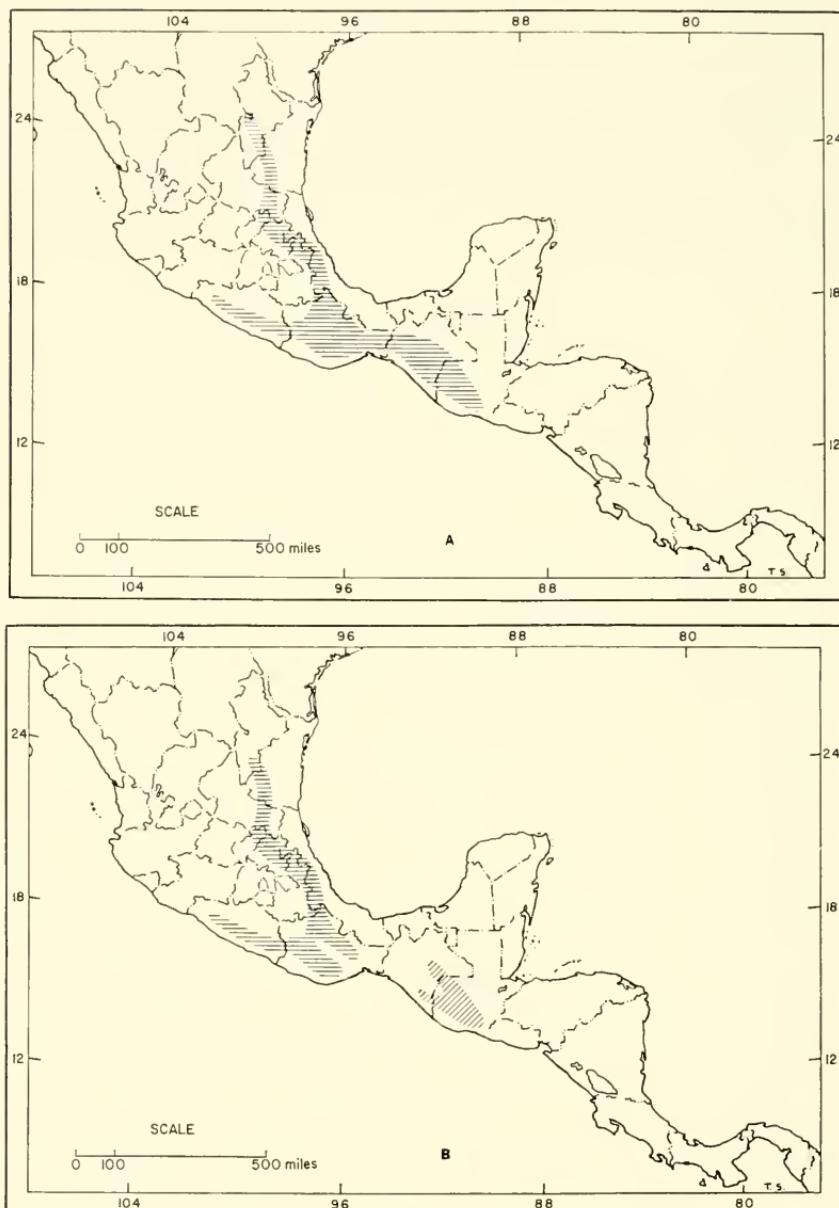


FIG. 20. Possible events resulting in speciation in the *Cryptotis mexicana*-group. A—Hypothetical distribution of *Cryptotis mexicana* or its precursor at some time during the Pleistocene. B—Increased aridity on the Isthmus of Tehuantepec isolates precursor of *goodvini* east of the isthmus.

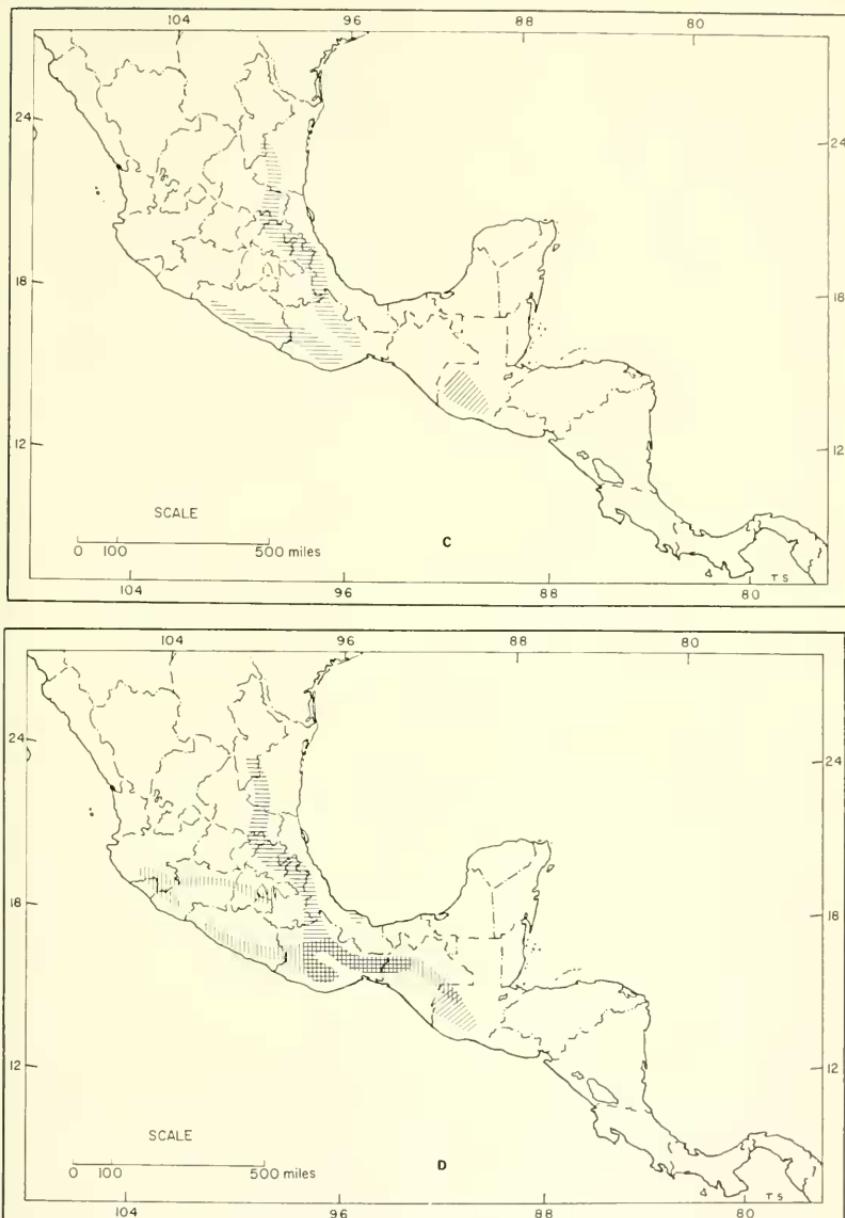


FIG. 20 (continued). C—Further increase in aridity eliminates gene flow across central Oaxaca, restricting *mexicana* to the Sierra Madre Oriental and Sistema Montañoso, and isolating the precursor of *goldmani* on the Sierra Madre del Sur. D—Distribution of *mexicana*, *goldmani*, and *goodwini* at present, showing zones of geographic sympatry (see text).

habitats within otherwise arid regions of southernmost Texas and northeastern, central, and western México primarily north of the Cordillera Volcánica; *C. p. soricina*, which is known only from mesic habitats in the Valley of Mexico; *C. p. pueblensis*, which occurs in habitats ranging from mesic grassland to cloud forest at middle elevations on mountains of eastern and southern México; *C. p. tropicalis*, which occurs in damp, tropical vegetation or pine-oak forests at middle elevations on highlands of easternmost Chiapas, Guatemala, and British Honduras; and *C. p. orophila*, which occurs primarily at middle elevations in grassy llanos, tropical vegetation, and cloud forests throughout the remainder of Central America as far south as western Panamá.

Cryptotis nigrescens was interpreted to consist of three well-differentiated subspecies: *C. n. mayensis*, which occurs at low elevations in habitats ranging from xeric scrub forest and grassy llanos to quasi-rainforest on the Yucatan Peninsula, and also is known from owl-pellet material collected in the Balsas Basin in Guerrero; *C. n. merriami*, which occurs primarily at middle elevations in cloud forests and pine-oak forests in northern Central America; and *C. n. nigrescens*, which occurs in habitats ranging from mid-elevation cloud forests up to the upper limit of forest vegetation in Costa Rica and Panamá.

Specimens of each of the late Pliocene taxa that have been referred to the tribe Blarinini of the subfamily Soricinae were examined, and their apparent relationships to extinct and extant species of *Cryptotis* were assessed. On the basis of information available from study of fossils and from assessment of apparent phenetic relationships, all Pleistocene and Recent species of *Cryptotis* pertain to one or another of four species-groups: the *parva*-group (including *parva* and *nigrescens*), the *mexicana*-group (including *mexicana*, *goldmani*, and *goodwini*), the *thomasi*-group (including all South American representatives of the genus), and a group of relict species (*gracilis*, *endersi*, and *magna*). In terms of zoogeographic affinities, these species-groups were subdivided into two geographic associations—those species (*magna*, *mexicana*, *goldmani*, and *parva*) that evolved and radiated primarily west of the Isthmus of Tehuantepec, and those species (*gracilis*, *endersi*, *goodwini*, *nigrescens*, and the *thomasi*-group) that evolved and radiated primarily east of the isthmus. The premise is set forth that climatic fluctuations and associated vegetative succession on the Isthmus of Tehuantepec has been an important factor in divergence of several species of *Cryptotis*, especially those of the *mexicana*-group.

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GAZETTEER

The following names of places and geographic or topographic features are those to which reference is made in this report. The spellings and coordinates given for localities were drawn from several sources: The American Geographic Society's "Map of Hispanic America . . .," scale 1:1,000,000, and its accompanying Index (1944); the *Atlas Geográfico de la República Mexicana*, scale 1:500,000; pertinent gazetteers of the U.S. Board on Geographic Names; a collection of maps entitled "Caminos de México," published by Compañía Hulera Euzkadi, S. A., third edition (1967); and various local road maps. When two or more maps disagreed as to spelling, the name judged to be in most common usage was listed. Names in brackets refer to other names or spellings frequently encountered in the literature or on maps. Latitude north of the equator and longitude west of Greenwich are provided for most localities; in several instances the coordinates given are indicated as only approximate, but represent my best estimate on the basis of information available. The sequence of countries, of states within México, and of localities within Mexican states and Central American countries is alphabetical. The appropriate departamento is listed for each locality in Central American countries; boundaries of several of those departamentos differ from one map to the next, but those designated herein were taken from the most recent maps available to me.

Two topographic features not listed below but mentioned in accounts require additional comment. First, the name "Sistema Montañoso" is an abbreviation for the more cumbersome "Sistema Montañoso Oaxaqueño-Poblano," as shown on several of the maps of "Caminos de México" (see above). The Sistema Montañoso is the portion of the Sierra Madre Oriental that extends southeastward beyond the Cordillera Volcánica across northeastern Oaxaca as far as the Isthmus of Tehuantepec. Most maps erroneously include that range of mountains in the Sierra Madre del Sur. Secondly, "Sierra de Xucaneb" refers to the highlands of central Alta Verapaz, Guatemala (Stewart, 1950:5).

BRITISH HONDURAS

Baking Pot, Cayo.— $17^{\circ} 12'$, $89^{\circ} 01'$.

Cayo, Cayo.— $17^{\circ} 00'$, $89^{\circ} 00'$.

COSTA RICA

Cartago, Cartago.— $9^{\circ} 51'$, $83^{\circ} 55'$.

Cerro Asunción, Cartago.—Approximately $9^{\circ} 01'$, $83^{\circ} 45'$.

Cerro Chirripó, San José.— $9^{\circ} 29'$, $83^{\circ} 30'$.

Cerro de la Muerte [Cerro Buenavista], Cartago.— $9^{\circ} 03'$, $83^{\circ} 45'$.

Cerro Estaquero, San José.—Approximately $9^{\circ} 27'$, $83^{\circ} 30'$.

Cerro Las Vueltas, Cartago.— $9^{\circ} 37'$, $83^{\circ} 52'$.

Cerro Tablazo, San José.— $9^{\circ} 49'$, $84^{\circ} 01'$.

Cinchona, Alajuela.—Approximately $10^{\circ} 18'$, $84^{\circ} 11'$.

El Muñeco, San José.— $9^{\circ} 47'$, $83^{\circ} 54'$.

Estrella, Cartago.— $9^{\circ} 52'$, $84^{\circ} 03'$.

Finca Coliblanca, Cartago.— $9^{\circ} 57'$, $83^{\circ} 53'$.

"Guarco."—According to Dr. Alvaro Wille T. (personal communication), of the Departamento de Entomología at the Universidad de Costa Rica: "The name 'Guarco' is a very old historical name used by the Spaniards to refer to the whole Cartago valley. The name is also applied to a particular area in the city of Cartago."

Heredia, Heredia.— $10^{\circ} 00'$, $84^{\circ} 07'$.

"Irazú Range," Cartago.—Probably somewhere on the southern or southwestern slopes of Volcán Irazú.

La Piedra, San José.— $9^{\circ} 29'$, $83^{\circ} 40'$.

Monte Verde, Limón.— $10^{\circ} 06'$, $83^{\circ} 26'$.

Pico Blanco, Limón.— $9^{\circ} 17'$, $83^{\circ} 04'$.

San Isidro de El General [San Indro], San José.— $9^{\circ} 59'$, $83^{\circ} 59'$.

San José, San José.— $9^{\circ} 56'$, $84^{\circ} 05'$.

San Pedro Montes de Oca [Montes de Oca], San José.— $9^{\circ} 56'$, $84^{\circ} 03'$.

Tilarán, Guanacaste.— $10^{\circ} 27'$, $84^{\circ} 59'$.

Volcán Irazú, Cartago.— $9^{\circ} 59'$, $83^{\circ} 53'$.

Volcán Turrialba, Cartago.— $10^{\circ} 02'$, $83^{\circ} 46'$.

Zarceo, Alajuela.— $10^{\circ} 11'$, $84^{\circ} 22'$.

EL SALVADOR

Apaneca, Ahuachapán.— $13^{\circ} 51'$, $89^{\circ} 47'$.

Cerro Cacaquatique, Morazán (on border with San Miguel).— $13^{\circ} 48'$, $88^{\circ} 14'$.

Hacienda [or Cerro] Montecristo, Santa Ana.— $14^{\circ} 25'$, $89^{\circ} 22'$.

GUATEMALA

Calel, Quezaltenango (on border with Totonicapán).— $15^{\circ} 02'$, $91^{\circ} 33'$.

Cobán, Alta Verapaz.— $15^{\circ} 29'$, $90^{\circ} 19'$.

Cumbre María Tucum, Totonicapán.—Approximately $14^{\circ} 50'$, $91^{\circ} 08'$.

Finca La Paz, San Marcos.—Approximately $14^{\circ} 50'$, $91^{\circ} 50'$.

Finca Xicacao, Alta Verapaz.—Approximately $15^{\circ} 31'$, $90^{\circ} 14'$.

Hacienda Chancol, Huehuetenango.— $15^{\circ} 25'$, $91^{\circ} 20'$.

Jacaltenango, Huehuetenango.— $15^{\circ} 40'$, $91^{\circ} 41'$.

La Primavera, Alta Verapaz.— $15^{\circ} 25'$, $90^{\circ} 29'$.

Mataquescuintla, Jalapa.— $14^{\circ} 31'$, $90^{\circ} 11'$.

Panajachel, Sololá.— $14^{\circ} 45'$, $91^{\circ} 09'$.

San Juan Ixcoy, Huehuetenango.— $15^{\circ} 38'$, $91^{\circ} 26'$.

Santa Cruz El Chol [El Chol], Baja Verapaz.— $14^{\circ} 57'$, $90^{\circ} 28'$.

Santa Elena, Chimaltenango.— $14^{\circ} 49'$, $91^{\circ} 02'$.

Tecpán, Chimaltenango.— $14^{\circ} 46'$, $91^{\circ} 00'$.

Todos Santos Cuchumatán [Todos Santos], Huehuetenango.— $15^{\circ} 30'$, $91^{\circ} 38'$.

Uaxactún, Petén.— $17^{\circ} 24'$, $89^{\circ} 37'$.

Volcán Santa María, Quezaltenango.— $14^{\circ} 45'$, $91^{\circ} 32'$.

Volcán Tajumulco, San Marcos.— $15^{\circ} 02'$, $91^{\circ} 54'$.

HONDURAS

Belén, Ocotepec.— $14^{\circ} 27'$, $88^{\circ} 27'$.
 Cerro Cantoral, Francisco-Morazán.— $14^{\circ} 22'$, $87^{\circ} 20'$.
 El Zamorano, Francisco-Morazán.— $13^{\circ} 59'$, $87^{\circ} 01'$.
 Lago de Yojúa, Cortes.— $14^{\circ} 45'$, $88^{\circ} 00'$.
 Las Flores, Gracias.— $14^{\circ} 39'$, $88^{\circ} 38'$.
 Llama, Santa Barbara.— $14^{\circ} 58'$, $88^{\circ} 12'$.
 Yuscarán, El Paraíso.— $13^{\circ} 55'$, $86^{\circ} 47'$.

MÉXICO

Campeche

La Tuxpeña [La Tuxpana].— $18^{\circ} 27'$, $90^{\circ} 04'$.

Chiapas

Bochil.— $16^{\circ} 59'$, $92^{\circ} 55'$.
 Comitán.— $16^{\circ} 15'$, $92^{\circ} 08'$.
 Escuintla.— $15^{\circ} 20'$, $92^{\circ} 38'$.
 Huixtla.— $15^{\circ} 08'$, $92^{\circ} 28'$.
 La Libertad.— $17^{\circ} 41'$, $91^{\circ} 43'$.
 Las Margaritas.— $16^{\circ} 20'$, $92^{\circ} 00'$.
 Prusia.— $15^{\circ} 44'$, $92^{\circ} 44'$.
 Pueblo Nuevo Solistahuacán [Pueblo Nuevo].— $17^{\circ} 08'$, $92^{\circ} 53'$.
 San Crostóbal de las Casas.— $16^{\circ} 45'$, $92^{\circ} 33'$.
 Union Juárez.— $15^{\circ} 04'$, $92^{\circ} 05'$.
 Villa Flores.— $16^{\circ} 14'$, $93^{\circ} 13'$.
 Yajalón.— $17^{\circ} 16'$, $92^{\circ} 20'$.

Coahuila

Melchor Múzquiz.— $27^{\circ} 53'$, $101^{\circ} 31'$.

Distrito Federal

Bosenchere.—Approximately $19^{\circ} 24'$, $100^{\circ} 08'$.
 Bosque Chapultepec, México.— $19^{\circ} 25'$, $99^{\circ} 10'$.
 Cañon Contreras.— $19^{\circ} 15'$, $99^{\circ} 15'$.
 Cerro de Santa Rosa.— $19^{\circ} 19'$, $97^{\circ} 17'$.
 Tlalpan [Tlalpam].— $19^{\circ} 17'$, $99^{\circ} 10'$.

Estado de México

Amecameca.— $19^{\circ} 07'$, $98^{\circ} 46'$.
 Cerro Ajusco.— $19^{\circ} 12'$, $99^{\circ} 15'$.
 Lagunas de Zempoala.— $19^{\circ} 03'$, $99^{\circ} 19'$.
 Nevado de Toluca.— $19^{\circ} 07'$, $99^{\circ} 45'$.
 Salazar.— $19^{\circ} 19'$, $99^{\circ} 24'$.
 San Juan Zitlaltepec.— $19^{\circ} 48'$, $99^{\circ} 08'$.
 Tlapacoyán [Tlapacoya].— $19^{\circ} 18'$, $98^{\circ} 55'$.
 Volcán Popocatépetl.— $19^{\circ} 02'$, $98^{\circ} 38'$.

Guanajuato

Guanajuato.— $21^{\circ} 01'$, $101^{\circ} 14'$.

Guerrero

Cerro Teotepec.— $17^{\circ} 27'$, $100^{\circ} 10'$.

Chilpancingo.— $17^{\circ} 33'$, $99^{\circ} 30'$.

Mexcala.— $17^{\circ} 56'$, $99^{\circ} 34'$.

Omilteme.— $17^{\circ} 33'$, $99^{\circ} 40'$.

Hidalgo

Acaxochitlán.— $20^{\circ} 10'$, $98^{\circ} 12'$.

Encarnación [Ferrería de Encarnación].— $20^{\circ} 53'$, $99^{\circ} 12'$.

Molango.— $20^{\circ} 48'$, $98^{\circ} 43'$.

Tenango de Doria.— $20^{\circ} 20'$, $98^{\circ} 12'$.

Tulancingo.— $20^{\circ} 05'$, $98^{\circ} 22'$.

Zacultipan.— $20^{\circ} 39'$, $98^{\circ} 37'$.

Jalisco

Autlán.— $19^{\circ} 45'$, $104^{\circ} 24'$.

Ciudad Guzmán [Zapotlán].— $19^{\circ} 45'$, $103^{\circ} 30'$.

Guadalajara.— $20^{\circ} 41'$, $103^{\circ} 20'$.

Huáscata.— $20^{\circ} 32'$, $102^{\circ} 14'$.

Mascota.— $20^{\circ} 33'$, $104^{\circ} 49'$.

Nevado de Colima [Volcán de Nieve].— $19^{\circ} 33'$, $103^{\circ} 37'$.

Ocotlán.— $20^{\circ} 21'$, $102^{\circ} 46'$.

Volcán de Fuego [Volcán de Colima].— $19^{\circ} 34'$, $103^{\circ} 36'$.

Michoacán

Cerro de Tancítaro.— $19^{\circ} 25'$, $102^{\circ} 18'$.

Ciudad Hidalgo.— $19^{\circ} 41'$, $100^{\circ} 32'$.

Colonia Ibarra.— $20^{\circ} 14'$, $102^{\circ} 34'$.

Cumuato.— $20^{\circ} 16'$, $102^{\circ} 34'$.

La Palma.— $20^{\circ} 09'$, $102^{\circ} 46'$.

Morelia.— $19^{\circ} 42'$, $101^{\circ} 11'$.

Pátzcuaro.— $19^{\circ} 30'$, $101^{\circ} 36'$.

Quiroga.— $19^{\circ} 42'$, $101^{\circ} 29'$.

Rancho Baralosa.—Approximately $18^{\circ} 50'$, $103^{\circ} 00'$.

Nayarit

Tepic.— $21^{\circ} 31'$, $104^{\circ} 54'$.

Oaxaca

Cerro San Felipe.— $17^{\circ} 11'$, $96^{\circ} 40'$.

Cerro Zempoaltepec [Zempoaltépetl or Cempoaltépetl].— $17^{\circ} 10'$, $96^{\circ} 00'$.

Choapan [Choapám].— $17^{\circ} 20'$, $95^{\circ} 57'$.

"Colonia Rudolfo Figueroa."—Probably near $94^{\circ} 15'$, $16^{\circ} 45'$; recorded as "20 km. NW Rizo de Oro, Chiapas."

Ixtlán de Juárez.— $17^{\circ} 20'$, $96^{\circ} 29'$.

Lachao.— $16^{\circ} 14'$, $97^{\circ} 08'$.

La Muralla.—Approximately $17^{\circ} 07'$, $97^{\circ} 40'$.

Llano de las Flores.— $17^{\circ} 30'$, $96^{\circ} 30'$.

Lovene.— $16^{\circ} 02'$, $96^{\circ} 12'$.

Mixteguilla [Magdalena Tequisistlán].— $16^{\circ} 22'$, $95^{\circ} 15'$.
 Oaxaca de Juárez.— $17^{\circ} 01'$, $96^{\circ} 43'$.
 Papalo Santos Reyes [Reyes].— $17^{\circ} 53'$, $96^{\circ} 48'$.
 Pluma Hidalgo [Pluma].— $15^{\circ} 55'$, $96^{\circ} 24'$.
 Puerto Escondido.—Approximately $15^{\circ} 50'$, $97^{\circ} 50'$.
 Putla.— $17^{\circ} 02'$, $97^{\circ} 56'$.
 San Agustín Loxicha [Loxicha or San Agustín].— $16^{\circ} 01'$, $96^{\circ} 36'$.
 San Andres Chicahuaxtla.— $17^{\circ} 10'$, $97^{\circ} 50'$.
 San Gabriel Mixtepec.— $16^{\circ} 05'$, $97^{\circ} 06'$.
 San Isidro.—Approximately $17^{\circ} 45'$, $96^{\circ} 42'$.
 San Juan Ozolotepec.— $16^{\circ} 08'$, $96^{\circ} 16'$.
 San Miguel Suchixtepec.— $16^{\circ} 05'$, $96^{\circ} 27'$.
 San Pedro Cajonos [San Pedro or Cajonos].— $17^{\circ} 10'$, $96^{\circ} 15'$.
 Santa María Ozolotepec.— $16^{\circ} 13'$, $96^{\circ} 22'$.
 Santos Reyes Nopala [Nopala].— $16^{\circ} 06'$, $97^{\circ} 10'$.
 Santiago Lachiquiri [Las Cuevas, Lachiquiri].— $16^{\circ} 41'$, $95^{\circ} 27'$.
 Sola de Vega.— $16^{\circ} 32'$, $96^{\circ} 58'$.
 Sta. Catarina Juguila [Juguila or Santa Catarina].— $16^{\circ} 15'$, $97^{\circ} 18'$.
 Tehuantepec.— $16^{\circ} 20'$, $95^{\circ} 13'$.
 Teotitlán del Camino.— $18^{\circ} 08'$, $97^{\circ} 07'$.
 Totontepec.— $17^{\circ} 13'$, $96^{\circ} 03'$.
 Tuxtepec.— $18^{\circ} 05'$, $96^{\circ} 06'$.
 Vista Hermosa.— $17^{\circ} 39'$, $95^{\circ} 15'$.

Puebla

Honey.— $20^{\circ} 15'$, $98^{\circ} 13'$.
 Huauchinango.— $20^{\circ} 11'$, $98^{\circ} 03'$.
 Metlatoyuca.— $20^{\circ} 45'$, $97^{\circ} 51'$.
 Villa Juárez [Xicotepec de Juárez or Juárez Xicotepec].— $20^{\circ} 17'$, $97^{\circ} 57'$.
 Xocoyolo.— $20^{\circ} 00'$, $97^{\circ} 32'$.
 Zacapoaxtla.— $19^{\circ} 53'$, $97^{\circ} 35'$.

Querétaro

Pinal de Amoles [Amoles].— $21^{\circ} 09'$, $99^{\circ} 37'$.

Quintana Roo

Laguna de Chichancanab.— $19^{\circ} 47'$, $88^{\circ} 42'$.

San Luis Potosí

Alvarez.— $22^{\circ} 02'$, $100^{\circ} 37'$.
 El Salto.— $22^{\circ} 36'$, $99^{\circ} 24'$.
 Huichihuayán.— $21^{\circ} 28'$, $98^{\circ} 57'$.
 Platanito.— $22^{\circ} 29'$, $99^{\circ} 26'$.
 Xilitla.— $21^{\circ} 23'$, $99^{\circ} 01'$.

Tamaulipas

Altamira.— $22^{\circ} 23'$, $97^{\circ} 56'$.
 Camargo.— $26^{\circ} 20'$, $98^{\circ} 50'$.
 Ciudad Victoria.— $23^{\circ} 44'$, $99^{\circ} 08'$.

Gómez Farías.— $23^{\circ} 03'$, $99^{\circ} 09'$.
 Matamoros.— $25^{\circ} 55'$, $97^{\circ} 30'$.
 Ocampo.— $22^{\circ} 50'$, $99^{\circ} 20'$.
 Piedra.— $23^{\circ} 30'$, $98^{\circ} 06'$.

Veracruz

Banderilla.— $19^{\circ} 35'$, $96^{\circ} 56'$.
 Boca del Río.— $19^{\circ} 06'$, $96^{\circ} 06'$.
 Catemaco.— $18^{\circ} 25'$, $95^{\circ} 07'$.
 Cerro Gordo.— $19^{\circ} 25'$, $96^{\circ} 42'$.
 Coscomatepec.— $19^{\circ} 04'$, $97^{\circ} 02'$.
 El Brinco.— $20^{\circ} 26'$, $97^{\circ} 36'$.
 Huatusco.— $19^{\circ} 09'$, $96^{\circ} 57'$.
 Jalacingo.— $19^{\circ} 48'$, $97^{\circ} 18'$.
 Jalapa.— $19^{\circ} 31'$, $96^{\circ} 56'$.
 La Joya.— $19^{\circ} 37'$, $97^{\circ} 02'$.
 Las Vigas.— $19^{\circ} 38'$, $97^{\circ} 05'$.
 Mecayucan.— $18^{\circ} 54'$, $96^{\circ} 14'$.
 Mirador.— $19^{\circ} 17'$, $96^{\circ} 54'$.
 Orizaba.— $18^{\circ} 51'$, $97^{\circ} 06'$.
 Potrera Vieja.— $18^{\circ} 52'$, $96^{\circ} 50'$.
 Teocelo [Texolo].— $19^{\circ} 23'$, $96^{\circ} 58'$.
 Tlapacoyan.— $19^{\circ} 58'$, $97^{\circ} 13'$.
 Volcán San Martín [Volcán de Tuxtla or San Martín Tuxtla].— $18^{\circ} 33'$,
 $95^{\circ} 13'$.
 Xico [Jico].— $19^{\circ} 25'$, $97^{\circ} 00'$.
 Zacualpan.— $20^{\circ} 28'$, $98^{\circ} 22'$.

Yucatán

Actun Spukil.—Approximately $20^{\circ} 34'$, $89^{\circ} 47'$.
 Chichén Itzá.— $20^{\circ} 41'$, $88^{\circ} 34'$.
 Mérida.— $28^{\circ} 58'$, $89^{\circ} 47'$.
 Uxmal.— $20^{\circ} 22'$, $89^{\circ} 46'$.
 Xbac.—Approximately $20^{\circ} 20'$, $88^{\circ} 55'$.

NICARAGUA

San Raphael del Norte, Jinotega.— $13^{\circ} 10'$, $86^{\circ} 05'$.
 Santa María de Ostuma, Matagalpa.— $12^{\circ} 57'$, $85^{\circ} 58'$.

PANAMÁ

Cerro Pirre, Darién.— $7^{\circ} 51'$, $77^{\circ} 44'$.
 Cerro Malí, Darién.— $8^{\circ} 07'$, $77^{\circ} 14'$.
 Cerro Punta, Chiriquí.— $8^{\circ} 53'$, $82^{\circ} 34'$.
 Cerro Punta-Boquete trail, Chiriquí.—Approximately $8^{\circ} 50'$, $82^{\circ} 30'$.
 Cerro Tacareuna, Darién.— $8^{\circ} 10'$, $77^{\circ} 18'$.
 Cilindro, Bocas del Toro.—Approximately $8^{\circ} 49'$, $82^{\circ} 24'$.
 Santa Clara, Chiriquí.— $8^{\circ} 51'$, $82^{\circ} 46'$.
 Volcán de Chiriquí, Chiriquí.— $8^{\circ} 51'$, $82^{\circ} 49'$.